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CHAPTER II

INFLUENCE OF THE DEGREE OF MATURITY OF THE SEED AT THE TIME OF HARVESTING UPON ITS "POTENTIALITY."

INTRODUCTION.

IN the previous chapter we have reviewed the literature dealing with the effect of parental conditions upon the "potentiality" of the seed, meaning by this not only the capacity of the seed for germination, but also the capacity of the resulting plant for growth and yield. In the present chapter we shall consider the influence of the degree of maturity of the seed at the time of harvesting upon the vigour and yield of the resulting plant.

Different degrees of maturity of the seed are determined (1) by harvesting the seed at a time prior to that of the natural shedding of the

seed, the degree of maturity depending also upon whether the seeds are harvested alone or whether they are harvested along with and allowed to dry in organic connection with the parent plant, and (2) by the weather conditions which obtain during the formation and ripening of the seed.

In dealing with immature seed of cultivated plants we have to distinguish in the first place between the immature seed as it comes from the plant with a relatively high moisture content, and the same seed after drying in air. This distinction is an important one, but the work dealing with the comparison of immature seed as it comes from the parent plant, and the same seed after air-drying has been for the most part confined to the question of capacity for germination.

The "Potentiality" of the Seed as influenced by the Time of Harvesting.

Mazé (19) described experiments with maize in which the germination of immature seeds straight from the parent-plant was compared with that of similar immature seed artificially dried.

The results of these experiments showed that the drying of the immature seeds did not affect their capacity for germination, which was 100 per cent. in both cases, but altered the physiological condition of the seeds in such a way that germination could take place quickly and normally. Thus, in the experiment quoted below (Table I) in which immature maize seed in the so-called milky stage was used, the sample previously dried over concentrated H_2SO_4 for 48 hours at 30° C. germinated fully in two days, whereas the sample which was not dried, but set to germinate immediately after removal from the parent plant, showed slow and sporadic germination extending over a period of 30 days.

Similar results were obtained with peas.

Table I.

Lot I consisted of a single vertical series of 19 grains, which were dried over concentrated H_2SO_4 for 48 hours at 30° C. before sowing.

Lot II consisted of a single vertical series of 20 grains (containing 45·6 per cent. moisture) detached from a head of maize. These grains were set to germinate *immediately* after removal from the parent-plant. They were placed one by one in test-tubes containing distilled water and provided with two cotton plugs, one of which supported the seed at the surface of the water whilst the other was used to keep out organisms from the air.

	Percentage of germinations after					
	2 days	7 days	14 days	22 days	28 days	30 days
Lot I	100 %	—	—	—	—	—
Lot II	—	15 %	30 %	55 %	95 %	100 %

Results of the same nature were recorded by Babcock (2) and by Eberhart (8). Babcock found (*l.c.* p. 129) that radish seeds taken from green pods, corn picked whilst the husks were still green, and sweet corn gathered whilst the kernels were still soft and milky failed to germinate when transferred direct from the parent plant to wet filter paper, whereas similar immature seeds after a preliminary exposure to warm dry air for a period of 10 days germinated quickly and completely in the normal way (Table II).

TABLE II.

Germination of Mature and Immature Seeds.

Influence of Maturity and Exposure to Air upon Germination.

Variety of seeds	State of maturity	Percentage moisture content	Germination percentage	
			On wet filters	In hydrogen peroxide
Yellow Dent Corn	Ripe, one year old	8·50	100 in 48 hours	100 in 48 hours
Yellow Dent Corn	Ripe, but soft	40·62	0	100 after 14 days
Yellow Dent Corn	Ripe, but soft	54·22	0	100 after 14 days
Stowell's Evergreen Sweet Corn	In edible condition	74·71	0	—
Radish	From green pods	—	0	—
Radish	From same green pods as above, but after 10 days' drying in air	—	100 in 48 hours	—

Eberhart (*l.c.*) found that whereas a sample of dead-ripe rye germinated immediately upon harvesting, the same grain, harvested in the milk stage, did not germinate until it had been stored for 40 days.

At this point it is interesting to enquire further as to the cause of the dormant condition of the maturing seed, and as to the reason why drying terminates this dormant condition and renders possible immediate germination and growth.

No satisfactory answer to these questions is as yet forthcoming. Mazé (20), however, in a more recent paper ascribed the dormancy of immature maize seeds placed under suitable germinating conditions immediately after gathering to the presence of small quantities of ethyl aldehyde in the cell-sap. He found small, but measurable, quantities of this substance in the freshly gathered green seed, but was unable to detect its presence in the same seed after drying. Mazé (*l.c.*) found also that when immature maize seed was artificially infected with various parasitic and saprophytic fungi (e.g. *Aspergillus*, *Mucor*, *Botrytis*, *Sclerotinia*, etc.) germination quickly ensued as compared with non-

infected control seed. Heads of maize picked before maturity were placed in a damp atmosphere under bell jars at the laboratory temperature. After an interval of 15 days it was found that the seeds, which had germinated, corresponded with the infected areas on the head as indicated by the presence of fungal mycelium. Mazé suggested that these organisms in some way destroyed the aldehyde, since the seeds which had germinated after inoculation were found to contain no aldehyde, whereas in a control head which was not inoculated a concentration of roughly $\frac{1}{50,000}$ aldehyde was found in the cell-sap (cf. also Mazé (18)).

Lastly, Mazé rules out direct oxidation processes as being responsible for the effect produced by desiccation. He dried some immature maize seeds in a vacuum and others in an atmosphere of CO_2 and found that in both cases the effect produced was similar to that produced by drying the seeds in air.

Babcock (2), however, believes that the characteristic effect of drying in rendering immature seeds capable of immediate germination is to be traced to an increase in direct "respiration," since the same effect can be produced without drying by treating the seeds with hydrogen peroxide. He suggests that the change brought about in the seed by increased respiration is the liberation of diastatic enzymes, which, according to Babcock, are normally absent from immature seeds.

His experimental data are meagre. There seems to be no criterion to distinguish cause from effect.

In a recent communication (Kidd (15)) it has been shown that the testa may play an important *rôle* with regard to the germination of immature or unripe seeds. In the case of *Brassica alba* and *Pisum sativum* it was found that the removal of the testa not only accelerated germination in the same way as drying, but also increased the germination percentage of unripe seeds as is shown in the following Table III. It is clear that the rest-period observed when attempts are made to germinate green immature seeds may be largely attributed to the presence of the living testa which, in the author's opinion, functions by limiting gaseous exchange to the embryo[1].

Although the point has not been fully investigated, the results so far obtained tend to show that there is no inherent rest-period in the developing embryo itself. Recent observations of Duggar (6) may be mentioned in this connection.

[1] The testa dies during the process of drying and its character as a membrane is thereby completely changed.

TABLE III.

Brassica alba.

Lot I consisted of 10 immature seeds.
Lot II consisted of 10 bare embryos from similar seeds.

Set on damp sand.

	Number of germinations after					
	2 days	4 days	6 days	7 days	12 days	18 days
Lot I	0	0	0	0	1	2*
Lot II	0	0	5	10†	—	—

* The remaining 8 ungerminated seeds finally died.
† Healthy plants.

Pisum sativum.

A { *Lot I* consisted of 20 immature seeds.
Lot II „ 20 bare embryos from similar seeds.

B { *Lot I* „ 20 less immature seeds.
Lot II „ 20 bare embryos from similar seeds.

C { *Lot I* „ 20 seeds picked 10 days later.
Lot II „ 20 bare embryos from similar seeds.

Set on damp earth and covered with a damp cloth.

		Number of germinations after		
		5 days	10 days	11 days
A	*Lot I*	0	1 (19 dead)	—
	Lot II	20	20 (18 vigorous plants)	—
B	*Lot I*	0	0 (all dead)	—
	Lot II	20	20 (vigorous plants)	—
C	*Lot I*	—	—	10 (10 dead)
	Lot II	—	—	20 (vigorous plants)

Duggar (*l.c.* pp. 387–8) states that "so far as ability to grow is concerned, no very narrow restrictions may be placed upon the stage of development of the seed, provided adequate and suitable nourishment can be given the young embryo. In a series of experiments recently carried out by the writer, whereby the young embryos were transferred from the developing seeds to sterile nutrient solutions, the results confirm the view that embryos thus treated are able to maintain themselves and sometimes able to develop mature plants."

The question now arises as to whether there is any difference in final yield from immature seeds as compared with that from fully ripe seeds. We have at the outset to distinguish between:

A. Immature seeds not dried (*i.e.* sown immediately after harvesting) as compared with fully ripe seeds.

B. Immature seeds separated from the parent stalk immediately after harvesting and then dried as compared with fully ripe seeds.

C. Immature seeds dried on the haulm after harvesting as compared with fully ripe seeds.

With regard to A no data have been found. In the case of B the question arises as to the effect of storage of the dry seed upon its potentiality. The general conclusion to be drawn from the experiments of numerous workers is clearly that immature seeds deteriorate much more rapidly than mature seeds when stored dry under similar conditions. For example, Hellriegel (12), working with rye, found the following percentages of germination after a period of dry storage of seeds harvested at different stages of maturity:

TABLE IV.

Stage of ripeness at which the seeds were harvested	Percentage germination
Contents of kernel watery	4·5
Milk stage	5·0
Dough stage	9·5
Yellow ripe stage	36·0
Dry ripe stage	84·0

And Nobbe (21), working with red clover, obtained the following results with ripe and unripe seeds respectively after 4 years' (*i.e.* 1870–1874) dry storage.

TABLE V.

A. Red Clover harvested in 1874 and tested in Dec. 1874.
B. „ „ 1870 „ „ Dec. 1874.

100 seeds were used in each experiment.

Kind of seed used		Percentage of germination after 13 days
A. Fresh seeds	Ripe	88
	Unripe	48
B. 4-year-old seeds	Ripe	58
	Unripe	6

Nobbe obtained similar results with other seeds, for example, *Brassica Rapa* var. *biennis*.

The experience of the Copenhagen Seed Testing Station as reported by the Director (4) leads to the same general conclusion, namely, that ripe seeds retain their germinating capacity longer than seeds which are less ripe.

The complication introduced by the harmful secondary effect of dry storage upon immature seeds must have entered into such experiments as those carried out by Lucanus. Lucanus (17) conducted a very elaborate series of experiments with rye, harvesting his seed at five different stages of maturity and dividing each harvest into four divisions, viz.:

Seeds immediately removed from the head (Section I of Table VI).

Seeds dried in the ear (Section II of Table VI).

Seeds dried in the ear on the stalk (Section III of Table VI).

Seeds dried in organic connection with the entire plant, the roots of which were placed in distilled water (Section IV of Table VI).

The results (Table VI) showed that in garden soil rich in humus the various stages of maturity of the seed had little or no effect upon the *yield per plant* as shown in his table, but a better *total yield* was obtained from

TABLE VI.

1. *Seeds sown in garden soil rich in humus.*

60 seeds sown in each experiment.

Stage of ripeness at which the seeds were harvested	Total yield after 3 months' growth				Yield per plant after 3 months' growth			
	I.	II.	III.	IV.	I.	II.	III	IV.
i. Seeds small, soft, and green. Straw not fully green	97 g.	719 g.	476 g.	617 g.	24·2 g.	15·3 g.	10·1 g.	15·8 g.
ii. Juice beginning to turn milky	13 g.	667 g.	685 g.	553 g.	13·0 g.	14·8 g.	14·5 g.	19·7 g.
iii. Juice thick and milky white. Straw still moderately green	86 g.	825 g.	785 g.	897 g.	12·3 g.	17·5 g.	14·5 g.	16·9 g.
iv. Seeds firmly attached to the glumes. Straw yellow and moderately dry. ("Gelbreife")	370 g.	1010 g.	380 g.	907 g.	16·8 g.	19·0 g.	13·6 g.	15·1 g.
v. Seeds free in the glumes. ("Ueberreife")	795 g.	880 g.	875 g.	1142 g.	14·2 g.	15·0 g.	17·5 g.	20·7 g.

2. *Seeds sown in a poor sandy soil.*

60 seeds sown in each experiment.

	I.	II.	III.	IV.	I.	II.	III.	IV.
i. Seeds small, soft, and green. Straw not fully green	3·0 g.	25 g.	35 g.	42 g.	1·5 g.	0·5 g.	0·9 g.	1·3 g.
ii. Juice beginning to turn milky	5·0 g.	52 g.	69 g.	93 g.	1·2 g.	1·3 g.	1·8 g.	2·0 g.
iii. Juice thick and milky white. Straw still moderately green	8·0 g.	135 g.	134 g.	252 g.	2·0 g.	2·8 g.	3·3 g.	5·1 g.
iv. Seeds firmly attached to the glumes. Straw yellow and moderately dry. ("Gelbreife")	82·0 g.	170 g.	90 g.	172 g.	3·9 g.	3·8 g.	6·0 g.	3·6 g.
v. Seeds free in the glumes. ("Ueberreife")	190·0 g.	117 g.	242 g.	145 g.	4·3 g.	3·0 g.	4·7 g.	3·3 g.

the riper seeds; this result was due to the larger percentage of germination in the case of the ripe seed.

In a parallel series of growth experiments conducted in very poor sandy soil, however, an effect of the degree of ripeness of the seed under these unfavourable growth conditions became visible in the yield per plant as well as in the total yield, better plants on the whole being produced from seeds gathered in the later stages of maturity.

The results obtained by Lucanus are borne out by those of Nowachi (22) with winter wheat grown in the field. Unfortunately his paper does not make it clear whether the immature seeds used by Nowachi which were not after-ripened (*i.e.* which were not allowed to dry off in organic connection with the parent-plant after harvesting) were sown green, or whether they were allowed to dry before sowing as was the case in the experiments conducted by Lucanus. His results, however, appear to show that the plants produced from the immature seeds were quite as good as those produced from the fully ripe seeds. In fact, the figures given in his table (Table VII) point to their being better.

It is seen that Nowachi found very little difference in the germination percentages.

The results of Lucanus and of Nowachi referred to above introduce the third point to be considered in discussing the question of immature seed. How far does the process of drying-off in organic connection with the parent-plant have any effect upon the "potentiality" of the

seeds owing to the transference of food-material from the haulm allowing them to advance a stage in maturity? Looking at the figures for yield per plant given in Table VI no important difference can be detected; this is not surprising in view of the fact that practically no difference is observable in yield per plant between plants from fully ripe and those from the most immature seeds.

TABLE VII.

Stage of ripeness at which the seeds were harvested	Average number of ear-bearing haulms		Average weight per plant		Germination percentage	
	I.	II.	I.	II.	I.	II.
Milk ripe (seeds still enclosed in the glumes; contents of seeds milky)	7·7	7·5	66 gms.	63 gms.	84	100
Yellow ripe (seeds yellow, shining; contents of seeds doughy)	5·4	5·2	44 gms.	44 gms.	100	98
Fully ripe	5·9	5·5	41 gms.	39 gms.	100	100
Dead ripe	5	—	43 gms.	—	98	—

I. Seeds, which were not after-ripened.
II. Seeds, which were dried on the haulm.

With regard to germination, on the other hand, the results obtained by Lucanus (Table VIII) certainly show that the immature seeds dried off in organic connection with the haulm retain their capacity for germination far better than those separated from the parent-plant before drying, except, of course, in the case of the fully ripe seeds[1].

Turning to the more recent investigations planned to determine whether the use of somewhat immature seed is to be recommended as an agricultural practice, we find that from the available evidence no good case can be made out in its favour.

Georgeson, Burtis, and Shelton (10) compared the yield from ripe wheat seed with that from seed harvested in the milk stage and found that the immature seed yielded 19·75 bushels of grain and 0·80 ton of straw per acre as compared with 22 bushels of grain and 1·04 tons of straw per acre produced from the mature seed. With oats, however, the same investigators (9) found that seeds harvested in the dough stage gave the best results, their figures being as follows (Table IX):

[1] Both Lucanus (16) and Nowachi (22) worked out elaborately the differences in weight and the detailed changes in contents which occur during the process of drying-off in seeds separated from the haulm immediately after harvesting as compared with those which take place in seeds allowed to dry off attached to the parent-plant.

TABLE VIII.

1. *Seeds sown in garden soil rich in humus.*

100 seeds sown in each experiment.

Stage of ripeness at which the seeds were harvested	Germinations			
	I.	II.	III.	IV.*
i. Seeds small, soft, and green. Straw not fully grown	6	82	85	67
ii. Juice beginning to turn milky	4	77	85	48
iii. Juice thick and milky white. Straw still moderately green	13	82	86	92
iv. Seeds firmly attached to the glumes. Straw yellow and moderately dry. ("Gelbreife")	37	88	50	100
v. Seeds free in the glumes. ("Ueberreife")	95	97	84	92

2. *Seeds sown in a poor sandy soil.*

100 seeds sown in each experiment.

	I.	II.	III.	IV.*
i. Seeds small, soft, and green. Straw not fully grown	3	80	70	55
ii. Juice beginning to turn milky	6	67	70	77
iii. Juice thick and milky white. Straw still moderately green	6	82	71	82
iv. Seeds firmly attached to the glumes. Straw yellow and moderately dry. ("Gelbreife")	35	80	27	82
v. Seeds free in the glumes. ("Ueberreife")	73	72	92	77

* The columns I, II, III, and IV correspond to those shown in Table VI.

TABLE IX.

Stage of ripeness at which the seed was harvested	Yield in bushels per acre
Seed in the dough stage	38·99
Seed in the hard dough stage	28·68
Seed ripe	26·66

Zavitz (24 & 25) gave the average results of five years' experiments with winter wheat in which the yield obtained from seed which was allowed to become thoroughly ripened before it was harvested was compared with that obtained from seed harvested at various stages of immaturity. The thoroughly ripened seed gave a better yield both of grain and of straw and a heavier weight of grain per measured bushel than that produced from grain harvested at either of the earlier stages of maturity.

The results of Kedzie's (14) experiments quoted by Duggar, in which the seeds used are characterised as having been harvested in the "milky juice," "dough," "full yellow ripe," and "dead ripe" stages respectively[1], showed the marked superiority of the ripe seed as compared with the unripe (Table X), and indicated that a slight advantage accrued from the use of the yellow ripe as compared with the use of the dead ripe seed, the yield being 30 bushels per acre from the former as against 28 bushels per acre from the latter.

TABLE X.

Stage of ripeness at which the seed was harvested	Yield per acre (in bushels)
Milky juice stage	11
Dough stage	25
Full yellow ripe stage	30
Dead ripe stage	28

Goff (11) in an experiment with Indian Corn extending over a period of five years found that the largest yields of corn and stalk were obtained from corn gathered slightly immature, and Tracy (23) bears this out in the case of Sweet Corn in a paper, dealing with the production of vegetable seeds, in which the conclusion is reached that for seed purposes the crop should be harvested as soon as the grain has fully passed into the dough condition. Goff found that the use of very immature seed gave smaller yields of corn and stalks, but slightly earlier maturity than fully mature seed.

The scanty results which have been recorded in the case of plants other than cereals with reference to the influence upon subsequent growth and yield of the use of immature seeds as compared with fully ripe seeds, appear to bear out the same general conclusions. Immature seeds germinate badly (probably due to changes during storage). They give rise to seedlings which may be in the first place less vigorous than those produced from mature seeds. But the resulting plants at a later stage differ very slightly from those arising from mature seed. The experiments of Arthur (1) and of Goff (11) with Tomatoes, in which a closer analysis of the growth and yield was made than in the case of cereals, indicate that the use of immature seed leads to an increase of reproductive parts in proportion to the vegetative parts. A greater number of fruits and seeds, but individually smaller and more rapidly ripening, were borne on the plants from immature seed.

[1] Janson (13) records in detail the changes which take place in the seed-reserves of oats and barley at different stages of maturity.

The "Potentiality" of the Seed as influenced by the Weather Conditions at the Time of Harvesting.

Nothing of a definite nature from the point of view of physiological pre-determination can be stated in this connection as there are no critical observations available. The general effect of dry climatic conditions during the maturation and harvesting of the seed crop will be to hasten maturity. Districts which have been found most valuable for industrial seed-production are those in which uninterrupted dry weather conditions prevail during late summer and far into the autumn. Wet weather conditions during maturation and at the time of harvesting will obviously not only affect the degree of maturity of the seed, but will also be unfavourable for gathering and storing the crop.

It has been shown repeatedly (*e.g.* Duvel (7); Dorph-Petersen (5)) that the deterioration of seeds during storage runs parallel to the percentage of moisture in the air-dry seed. A slight difference in the amount of water present in the air-dry seed at the time of storing causes marked differences in its subsequent germination capacity, the lower water-content being in the majority of cases the best.

Duvel's (7) conclusion is that the deterioration of seeds in dry storage is due to oxidations (cf. also Babcock (2); Becquerel (3), and others). The amount of CO_2 produced by seeds stored air-dry can be correlated with their percentage moisture-content and with the loss of vitality subsequently observed.

Conclusions.

A consideration of the results reviewed above makes it clear that the question as to whether differences in the resulting plant are pre-determined by the use of seeds differing in degree of ripeness cannot be regarded as satisfactorily answered in the case of any single species.

This is due to the fact that all the recorded comparisons between plants grown from immature seeds and plants grown from mature seeds appear to have been complicated by some period of storage. Immature seeds are less tolerant of storage in the dry condition than mature seed, so that in the case of the comparisons which have been made, the total yields from immature seeds are usually less than those from mature seeds owing to the fact that a smaller percentage of the immature seeds germinate.

When in such experiments comparisons are made between yield per plant, however, the difference in favour of the plants from mature seeds

tends to disappear or even to be reversed. This result may be significant, but it must be remembered that while the yield per plant in the case of the mature seeds represents an average based on a whole population (*i.e.* both vigorous and weak plants), the yield per plant in the case of the immature seeds, on the other hand, probably represents an average based on the more vigorous members of the population only, the others having perished during storage in the seed stage.

From the point of view of the grower seed harvested at a stage somewhat previous to maturity may, under certain conditions, give a better yield than seed allowed to become dead-ripe upon the parent-plant; but it must be borne in mind that immature seed does not withstand storage as well as seed which has been allowed to become fully ripe, so that—as a general practice—the use of immature seed is not to be recommended.

(*To be continued.*)

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THE STRUCTURE, BIONOMICS AND FOREST IMPORTANCE OF *CRYPHALUS ABIETIS* RATZ.

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Amongst systematists who have worked on the Scolytid or bark-boring beetles there are great differences of opinion as to the limits of the genus Cryphalus. Following Fowler[1] the genus comprises 24 different species which are widely distributed throughout the world. In his *Coleoptera of the British Isles* he records six different species some of them amongst the smallest of our indigenous beetles. All of them are of economic importance in forestry. Of our native species two, *Cryphalus abietis* Ratz. and *Cryphalus piceae* Ratz., choose as their hosts coniferous trees; the others are found on broad-leaved species.

Till quite recently these two coniferous species were considered rare in Britain but the increasing number of records of *C. abietis* in Scotland makes it no longer possible to describe this beetle as rare.

In view of new schemes of afforestation it is urgent that we should have exact information on the relative forest importance of the various insect enemies of trees. Further, for purposes of intelligent control a knowledge of the species in its various stages and of its life-history and habits is necessary. With these principles in view the following research on *C. abietis* was undertaken.

The research is based on an investigation of its life-history and habits, carried out by means of observations and control experiments, conducted in the open at Aboyne, Aberdeenshire, and Banchory-Devenick, Kincardineshire, and of a series of anatomical studies and breeding experiments made in the laboratory at Edinburgh University on and with material collected in the woods in the vicinity of the places named above and in the neighbourhood of Edinburgh.

Following Fowler the genus Cryphalus possesses the following characters: (1) eyes entire or slightly emarginate, (2) antennae with the sutures of the club distinctly marked, the club itself being somewhat variable in shape, (3) thorax tuberculate in front, margined at base,

[1] Fowler's *Coleoptera of the British Isles*, v, 428–430.

(4) scutellum small punctiform, (5) elytra not excavate at apex, clothed with a scale-like pubescence and sometimes in addition with fine raised hairs.

DESCRIPTION OF *C. ABIETIS* RATZ.

The following is Fowler's[1] description:

C. abietis Ratz. (Fig. 1). Oblong, subcylindrical, compressed and very convex: fuscous or fuscous-brown, dull, antennae and legs reddish-

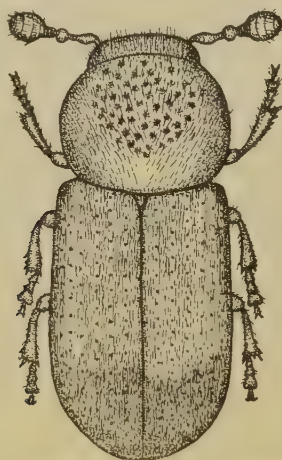

Fig. 1. Adult of *Cryphalus abietis* Ratz. (greatly magnified).

brown, club of the former usually darker, rounded at apex: thorax subglobular, very finely punctured at sides and behind, front part confusedly granulate: elytra rather more than double as long as thorax with distinct punctured interstices, covered throughout with extremely short scale-like hairs, and also very diffusely with short erect hairs, which are wanting behind: the colour of the antennae and the legs is somewhat variable: the species may easily be recognised by the tubercles on the anterior portion of the thorax being few in number and irregular in their distribution and by the regular comparatively strong rows of punctures and very short pubescence of the elytra. Length $1–2\frac{3}{4}$ mm.

My own examination of numbers of *C. abietis* leads me to emphasise the following characters:

(1) Club of antennae rounded at apex, antennal funicle four-jointed (Fig. 2).

[1] Fowler's *Coleoptera of the British Isles*, v, 431–432.

(2) Tubercles on prothorax irregular in distribution (not in concentric circles) and wide apart.

(3) Elytra covered with very short scale-like hairs, their interstices with a diffuse row of short erect hairs, which are absent on the apical parts.

From the measurement of a large number of specimens of various origin I find the average length to be 1·75 mm.

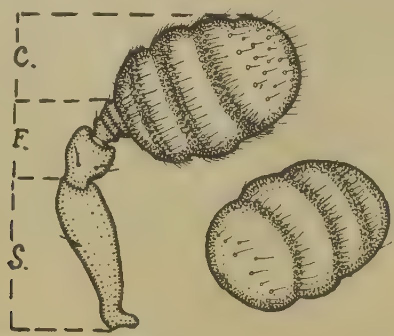

Fig. 2. Antenna of *Cryphalus abietis* Ratz. Posterior face of club is shown on the right (both greatly magnified). *C.* = club; *F.* = funicle; *S.* = scape.

SEXUAL DIFFERENTIATION IN *C. ABIETIS*.

There are no reliable external differentiating sex-characters although sometimes the female is slightly larger than the male.

Owing to the close resemblance in feeding habits, similar size, and external naked eye appearance of *C. abietis* and *C. piceae*, these two species may be readily confused.

I have compared by aid of the binocular microscope my *C. abietis* with *C. piceae* from Central Europe in Dr Stewart MacDougall's collection and give in tabular form the outstanding differences between the two beetles.

C. abietis	*C. piceae*
Tubercles on prothorax irregular in their distribution (not in concentric circles) and wider apart.	Tubercles on prothorax fairly regular in their distribution (in concentric circles) and closer together.
Sides and posterior margin of prothorax bear no marked greyish-white hairs.	Sides and posterior margin of prothorax bear long raised greyish-white hairs.
Interstices of elytra covered throughout with scale-like hairs, and each has a row of diffuse short erect greyish-white hairs which are absent on the apical parts.	Interstices of elytra covered with a few scale-like hairs and each has a row of long, raised, greyish-white hairs, which are most marked on the lateral margins and apical portions of the elytra.

EGG OF *C. ABIETIS.*

The egg is oval in shape, whitish in colour, translucent; and has a smooth shiny surface. The egg measures about ·6 mm. in length and a little less than ·3 mm. in breadth.

LARVA OF *C. ABIETIS* (Fig. 3).

The larva, in general appearance, is typically Scolytid. It is a soft legless grub, with a curved body. The colour of the larva is yellowish-white save the hard chitinous head and mouth-parts which are darkish brown. The body is much wrinkled, with fine hairs scattered over it.

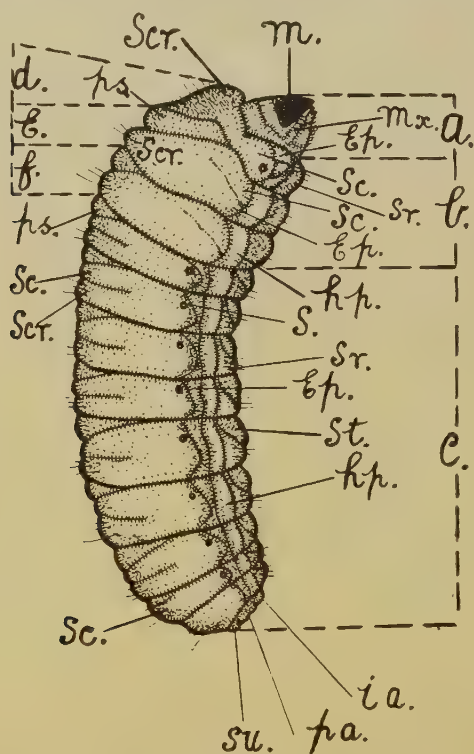

Fig. 3. Larva of *C. abietis*, side view (greatly magnified).

The larva is made up of the oblong chitinous head-piece—two-thirds of which is retractile within the first body segment or prothorax—and thirteen distinct body segments. The first three body segments form the

thorax, the other ten the abdomen. The thoracic segments are larger than the abdominal ones. The first segment of the thorax is more flattened dorsiventrally than the others and bears on its dorsal surface a rectangular patch covered with a felt of fine reddish-brown hairs. The 8th and 9th abdominal segments are much smaller than the others. In a ventral view (Fig. 7) the 10th or last segment is seen to consist of four distinct lobes around the anus. Spiracles, circular in shape, are present on the first thoracic segment and the first eight abdominal ones. The length of the full-grown larva is, on an average, 2·25 mm.

HEAD OF LARVA (Fig. 4).

With the aid of a binocular microscope the following parts can be made out in a dorsal view.

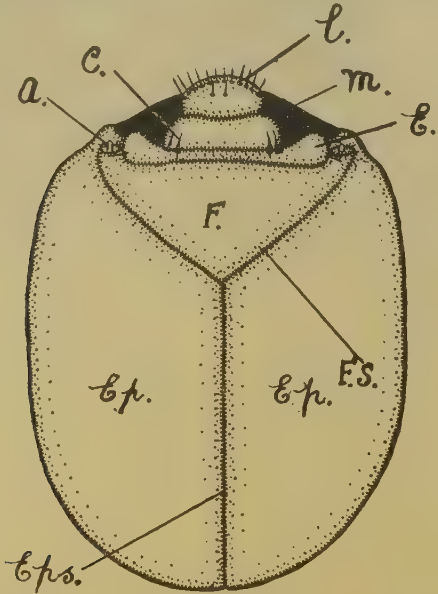

Fig. 4. Head of larva of *C. abietis* seen from above (greatly magnified).

Most anteriorly lies the labrum (*l.*) or upper lip which bears a number of fairly strong bristles on its front margin. Posterior to the labrum lies the clypeus (*c.*) while still further back may be seen the epistome (*E.*), a thickened band of chitin carrying a few strong bristles and forming a

support to the clypeus. At each end of the epistome lies a single-jointed antenna (*a.*) sunk in a pit. In each pit, externally to the antennae four chitinous bristles are usually placed. These details are more clearly shown in the enlarged view of the epistomal region (Fig. 5). In this figure *Ep.* stands for epistome.

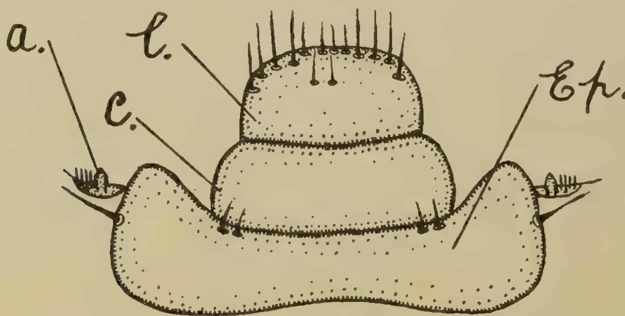

Fig. 5. Region of epistome of *C. abietis* larva (greatly magnified).

Posterior to the epistome and adjacent to it lies a triangular area, the frons (*F.*), bounded on each side by the frontal sutures (*F.S.*). On each side of the frontal sutures lies the epicranium (*Ep.*), a large area which occupies the greater portion of the surface of the head. The epicranium in turn is divided posteriorly into two parts by the epicranial suture (*Ep.s.*).

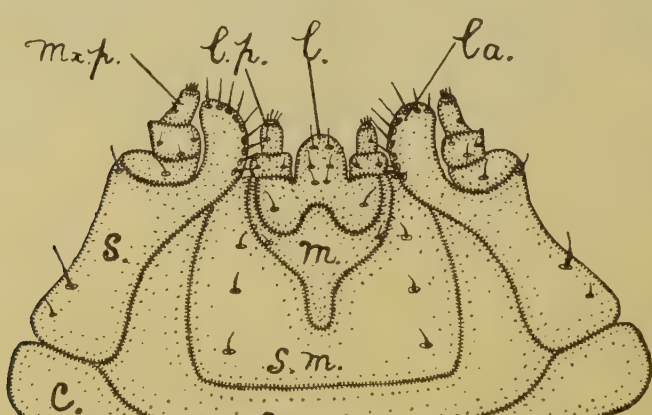

Fig. 6. Maxillae and labium of larva of *C. abietis* (greatly magnified).

On each side of the labrum and partly overlapped by it, are the mandibles. Each mandible (*m.*) is dark brown in colour, highly chitinized and bears three teeth, the posterior one being the smallest.

On the ventral aspect of the head lie the maxillae (Fig. 6).

1st Maxillae: These lie one on each side of the labium and are composed of the usual three parts: posteriorly the cardo (*c.*), more anteriorly the stipes (*s.*), bearing a three-jointed maxillary palp (*mx.p.*) and a few scattered bristles, and thirdly the lacinial lobe (*la.*) which has a number of stout chitinous bristles on its outer margin.

2nd Maxillae: In the centre of the field lies the labium or fused 2nd maxillae, made up of the mentum (*m.*) with two labial palps (*l.p.*) each two-jointed and with the ligulae (*l.*) lying between them. Posterior to the mentum is the submentum (*s.m.*), often indistinct from the submental area (*s.a.*) which lies still further back.

THE THORAX (Fig. 3 *b*).

The thorax of the larva is made up of the usual three segments, namely the prothorax, lying behind the head, the mesothorax, and the metathorax.

In a side view of the prothorax (Fig. 3 *d*) one can make out the following five folds: the scutellar (*scr.*) forming the dorso-lateral portion and bearing the rectangular patch of fine hairs already referred to; the scutal (*sc.*) bearing a spiracle on its most ventral portion; the epipleural (*ep.*) and the hypopleural (*hp.*) forming the lateral portion (the two last-named folds are more ventral than the first); the sternellar (*sr.*) forming the ventral portion.

The mesothorax (Fig. 3 *e*) in side view shows six folds: the prescutal (*ps.*) forming the anterior dorsal portion: the scutellar (*scr.*) forming the dorso-lateral portion: the scutal (*sc.*), epipleural (*ep.*) and hypopleural (*hp.*) forming the lateral portion; the sternellar (*sr.*) forms the ventral portion. There are no spiracles borne by the mesothoracic segment. The metathoracic segment (Fig. 3 *f*) is similar to the mesothoracic in structure and is of a corresponding size and shape.

THE ABDOMEN (Fig. 3 *c*).

The first seven abdominal segments are similar in structure although they vary in size. In side view each segment shows seven folds: the prescutal (*ps.*), scutal (*sc.*) and scutellar (*scr.*) form the dorso-lateral portion; the epipleural (*ep.*) and the hypopleural (*hp.*) form the lateral portion: while the sternal (*st.*) and the sternellar (*sr.*) form the ventral portion. On each segment, between the epipleural (*ep.*) and the scutal

(*sc.*) and scutellar (*scr.*) folds there is a deep crescent-shaped hollow or groove; on the anterior dorsal side of this groove lies a spiracle (*s.*).

The 8th abdominal segment, in side view, shows a similar composition to the first seven segments except that the prescutal and the scutellar folds are just traceable. The 9th abdominal segment is similar to the 8th except that the prescutal fold is absent and there are no spiracles. The 10th segment, in side view, shows three lobes surrounding the anus; the infra-anal lobe (*ia.*) situated ventral to the anus; the supra-anal (*su.*) dorsal and the para-anal (*pa.*) between the above two.

Looking at the larva from the ventral side (Fig. 7) two other folds may be seen on the thoracic segments, namely the sternal (*st.*) and the poststernellar (*ps.*).

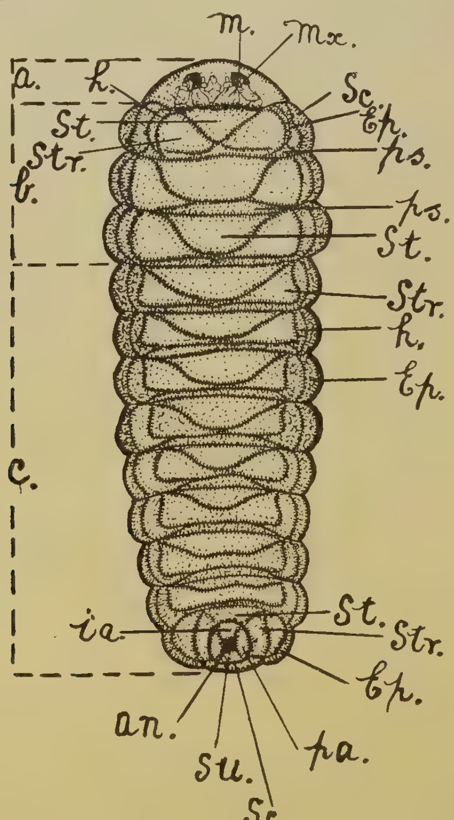

Fig. 7. Ventral aspect of larva of *C. abietis* (greatly magnified).

In a ventral view of the abdomen (Fig. 7 *c*) one other fold, namely the poststernellar, is discernible in addition to those already seen in the side view. The poststernellar fold is present in all the abdominal segments except the last three: in the 8th and 9th it is absent: in the 10th both poststernellar and sternal folds are wanting. In this figure *Str.* stands for sternellar fold and *h.* for hypopleural fold.

THE PUPA OF *C. ABIETIS.*

At first the pupa has the general colour of the larva but soon darkens, the mandibles being the first of the appendages to reveal themselves as two brownish patches.

In a dorsal view of the pupa the main divisions of the body are visible. On the vertex or front portion of the head one can make out a few frontal spines. These are fairly conspicuous and are widely separated.

On the sides of the pronotum may be seen a few scattered spines. Lying at the base of the elytra is the scutellum which is easily distinguishable.

Rows of dorsal and pleural spines are absent on the dorsal and lateral surfaces of the abdominal segments, a noteworthy feature as these spines are usually present on the corresponding parts of many Scolytid pupae.

On the ventral aspect of the pupa the usual appendages on the several divisions of the body can be made out. On the head portion the antennae and at the base of the antennae the eyes; lying posteriorly the gena or cheek region between the antenna and the labrum; mandibles, 1st maxillae and labium are also distinguishable.

The legs are folded along the surface of the body, the last pair for the most part obscured from view by the overlapping elytra. On the abdomen only the last few segments are visible in the ventral view; the 9th bearing two prominent fleshy projections or spines is the most conspicuous one. The presence of these spines is characteristic of Scolytid pupae.

On each side of the body lies an elytron or wing cover from under which projects the tip of a flying wing.

THE BROOD GALLERIES OF *C. ABIETIS* (Fig. 8).

In some of our bark-boring genera the parent beetles make a comparatively straight strong burrow or mother gallery. Unlike these the typical mother gallery of *C. abietis* rather takes the form of a circular burrow which is cut or gnawed round the base of a branch or twig. If

the branch round which the burrow is cut happens to be a fairly strong one it may be only partially eaten round. On the other hand, if the branch be weak, as is very often the case, the burrow completely girdles the branch. The length of the gallery varies. When the mother gallery is short it is broader, when long it is usually narrower. On an average the distance between the beginning of the mother gallery and its termination, measured along its course, is about $\frac{3}{4}$ inch in length, while in breadth it measures from $\frac{1}{8}$–$\frac{3}{16}$ inch.

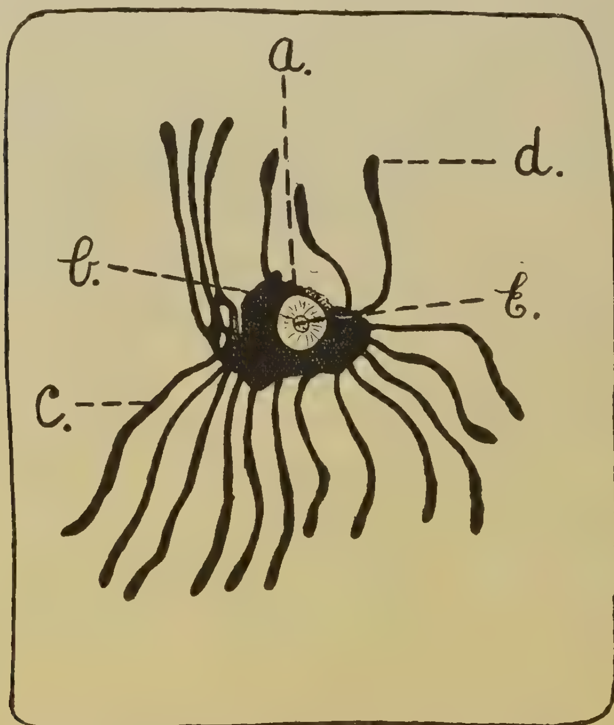

Fig. 8. Typical brood galleries of *C. abietis* on a branch of Silver Fir (*Abies pectinata* D.C.). Note how the mother gallery is cut round a smaller branch (*E.*). *a.* = beginning of mother gallery; *b.* = mother gallery widened in parts through the feeding of the young larvae; *c.* = larval gallery; *d.* = pupal bed; *E.* = base of smaller branch round which mother gallery is cut.

The larval galleries naturally run almost at right angles to the mother gallery, radiating out from it on all sides. Some of these larval galleries

run vertically upwards along the main branch, others run vertically downwards, while others run obliquely. Very frequently the larval galleries run along the branch or twig the base of which has been girdled by the mother gallery. The larval galleries, like the mother galleries, vary considerably in length. The shortest one I have measured was about ½ inch in length, while the longest was about 1½ inches.

As is usually the case in monogamous species of Scolytids the female does all the work in the cutting of the mother gallery, right from the entrance hole to its terminating point. In a few cases, however, prior to the disappearance of the female underneath the outer bark I found the male cutting a separate hole close beside her, evidently feeding on the gnawed material. As soon as the female had made a burrow long enough to accommodate herself underneath the bark the male at once repaired to her aid and helped her to widen the mother gallery, following her closely, gnawing first at one side of the gallery then at the other. The chief work of the male however is to throw to the outside of the entrance hole of the gallery the fine bore dust, shovelling it out with his legs. The sexes meet on the surface of the bark.

In many genera of Scolytids, *e.g.* Myelophilus and Tomicus, the eggs laid by the female are deposited in notches cut by her, as she bores, at more or less regular intervals along both sides of the mother gallery. In the case of *C. abietis* the eggs are laid irregularly and no notches are cut by the female; in fact the eggs usually occur in batches. In some cases I found that the female after she had cut a part of the burrow turned back towards the entrance hole and then laid four eggs; after she had laid this set of eggs she again proceeded to tunnel her gallery, returning after a time to lay another set of eggs. The female lays from 14 to 24 eggs and takes from 5 to 7 weeks to complete her gallery.

The larvae when hatched burrow irregularly for some time, eating along the sides of the mother gallery and usually altering its shape. As a result it is often impossible to determine the original shape of the mother gallery after the eggs have hatched. After boring along the sides of the mother gallery for some time the larvae separate and each gnaws a separate burrow in the inner bark layers, feeding on the gnawed material. This gnawed material is passed through the alimentary canal and the undigested waste material fills the burrow behind the larva.

The mother galleries never penetrate the sapwood but show on the inner bark layers. The young larvae while feeding in their tunnels do not cut the sapwood but for some time prior to pupation they often do groove the sapwood. In other cases the larvae do not groove the

sapwood at all until about to pupate when they invariably cut a pit or bed in the outer surface of the sapwood. This bed or pit excavated by larvae about to pupate lies in no constant direction. Sometimes it may be in the vertical direction, at other times horizontal, and at others oblique.

Thus when a piece of bark is removed from an infested branch the brood galleries cannot be traced on the sapwood at all. As a rule one can trace only that portion of the larval galleries which was cut previous to pupation and the pupal bed or pit on the exposed wood surface. While this is the typical occurrence other appearances are possible. For example, in further observations I noticed that when the bark was somewhat thick, as in the case of strong branches, the larval galleries often did not groove the sapwood at all and usually on these branches pupation took place in the bark. Where the bark was thin on the other hand, as on twigs and on small branches, the larval galleries throughout their entire length grooved the sapwood deeply while the pupal beds in such places were very marked on the surface of the sapwood. As a result when the outer bark was removed from an infested branch with fairly thick bark only the pupal beds could be traced. While if this same operation was performed on an infested twig or weak branch when the bark was thin the larval galleries and pupal beds could easily be traced on the wood surface.

After the period of pupation has passed the young imagos first feed on the patches of the inner bark which surround their pupal beds and then finally bore to the outside through the bark and issue by the small exit holes.

As I point out later in this paper the parent beetles do not all die after egg-laying but in many cases feed anew prior to a possible second egg-laying. I have frequently found these old parent beetles after their egg-laying has been completed cutting galleries which resembled in shape and in direction larval ones.

Irregular Galleries.

Overcrowding of both mother and larval galleries is not uncommon and takes place on badly infested stems and branches (Fig. 9) with the result that the galleries may be very irregular both in shape and in direction. In many cases it is extremely difficult or impossible to trace, in the confused workings, individual galleries. As a rule on badly infested branches the larval galleries are much shorter than those found on not so badly attacked ones. As a common instance of overcrowding we

may take the case figured here, where the bases of two branches of the same whorl have each been girdled by mother galleries. Here the larval

Fig. 9. Piece of branch of Silver Fir with irregular brood galleries of *C. abietis* due to overcrowding. A side view is shown of the bases of two small branches which have been girdled by mother galleries—represented in the figure as dark projecting portions one on each side of the main branch. Note how the larval galleries arising from the mother galleries have intermingled and so have completely girdled the main branch. The original shape of the mother galleries is here obliterated completely by young larval galleries (dark patches on the main branch) running together; later the larval galleries separate, running upwards and downwards on the main branch.

galleries which arise from each set of mother galleries usually intermingle and as a result completely girdle the main branch. Further in such cases (see figure) it is quite impossible to determine from which set of mother galleries the larval ones arise.

Even more confused workings than the above example are quite common. For instance, where two or more females have chosen the same axil of the branch or twig for brood purposes, the entrance holes of the mother galleries are very near to one another, which leads to

great confusion of mother galleries and larval galleries. The galleries in such cases intersect each other in all directions, forming a network underneath the outer bark layer.

Again where the bases of branches of a whorl have already been badly infested by beetles other parent beetles may commence boring brood galleries on the main branch between the whorls. This occurrence is very common on badly infested stems and branches and leads to still greater confusion of brood galleries.

An exceptional irregularity was found where a number of males and females had used the same entrance hole from which to bore their galleries. Each pair of parent beetles entered underneath the bark by this common entrance hole and immediately proceeded to make a separate mother gallery. These mother galleries radiated out in all directions from the common entrance burrow (see Fig. 10). I have taken as many as five pairs of beetles from such a set of galleries.

Fig. 10. Irregular mother galleries (not finished) on a piece of Silver Fir stem.

In dealing with the brood galleries of *C. abietis* it is quite impossible in most cases to trace either mother or larval galleries on the removal of the outer bark.

Instead one usually finds all the inner bark layers converted to dust by the work of parent beetles and their larvae. The best way to ascertain the shape of a typical mother gallery is to dissect the gallery immediately after the female has completed her egg-laying and before any of the eggs have hatched. To trace the larval galleries accurately it is essential in most cases to follow up the larvae as they tunnel their respective galleries.

LENGTH OF LIFE-CYCLE IN A SINGLE GENERATION.

Many observations repeated under different conditions proved to me that the period of the life-cycle from the laying of the egg to its culmination in the adult stage was extremely variable. The time varied according to the season of the year at which the eggs were laid, the quality of the food material, and the position of that material with relation to the sun: and consequently the environmental temperature.

In the vicinity of Aboyne, Aberdeenshire, field observations were carried out in early April, 1917, in Silver Fir woods badly infested with *Cryphalus abietis*. Careful examination was made of all likely places for females to have chosen for new brood galleries but no adults were found at work. The weather up to this time had been exceptionally unfavourable.

On the 28th September, 1916, however, I had collected some badly infested material consisting of branches and twigs from these same Silver Fir woods. Examination of this material at the time of collection showed that *Cryphalus abietis* was present underneath the bark layers in exceedingly large numbers both as immature fresh young adults and as larvae. This badly infested material—referred to later in this paper as my "stock material"—was kept in the open air throughout the winter months and examined at intervals. On the 20th of April, 1917, one adult issued. Several more adults issued up to 27th April, 1917. Some of these were killed and dissected for the study of their reproductive organs but 50 others were liberated in a muslin bag containing a few branches of Silver Fir and Spruce. These branches had been paraffined at their cut ends to keep them from becoming too dry. This bag was then closed and placed in the open air. Three days later, *i.e.* on 30th April, 1917, the branches in the bag were carefully examined. Some females had just commenced to bore into the Spruce and Silver Fir branches and in a number of cases the male beetle was found resting on the surface of the bark close by the female.

In another experiment carried out in a similar method and under similar conditions 60 adults were liberated on May 2nd, 1917. Dissections of many mother galleries were made at intervals with a view to collecting all the data possible on the making of the gallery and the egg-laying.

In one dissection made 16 days after the commencement of the gallery I found one egg laid while in another four eggs were laid by the end of a month.

The incubation period of the eggs was on an average 10 days. Large numbers of adults continued to escape from my "stock material" up to June 15th, 1917.

The time taken by the parent beetles to bore the mother gallery varied from 5 to 7 weeks.

Some larvae fed for 69 days and then pupated, the pupal period lasting about 29 days.

Thus in the case of eggs laid on June 4th, 1917, *i.e.* a month after the commencement of the mother gallery, the total period until the imago stage was reached on September 21st, 1917, was 108 days.

In my control experiments in natural conditions, some badly infested Silver Fir branches in the woods at Aboyne examined on June 26th, 1917, were found to contain hundreds of eggs of *C. abietis* and in many cases the females had not yet completed their egg-laying. These branches were examined at intervals throughout the summer and the length of the various stages was found to be as follows, viz. egg on an average 10 days: larva 71 days: pupa 22 days. That is to say the life-cycle from the egg stage at the end of June to the adult stage on September 27th was 93 days.

While in the above cases many individuals of the same brood reached the adult stage in the average period, quite a number of others were still in the larval stage at the end of September, 1917, and hibernated as larvae.

As showing the variations found in the length of the life-cycle I have set out in the following diagrams the life-cycles which I met with in my control experiments and in the open.

Diagram A.

+ = adult. • = egg. – = larva. ○ = pupa.

Year	Jan.	Feb.	March	Apl.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1916	...	...	...	...	+ •	– –	– –	– ○	○ +	+	+	+
1917	+	+	+	+	+ •	• –	–	– ○	○ +	...	...	...

Diagram B.

This diagram is for comparison with Diagram A showing the possible development of the last laid eggs of the same beetles.

Year	Jan.	Feb.	March	Apl.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1916	...	...	...	...	+ +	•	–	–	–	–	–	–
1917	–	–	–	–	–	○ ○	+ +	...	...	...	...	...

Diagram C.

Life-cycle found where the brood material was lying under dense shade and hence summer temperature low—here whole of young brood hibernates as larvae.

Year	Jan.	Feb.	March	Apl.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1916	...	...	...	...	+ •	• –	–	–	–	–	–	–
1917	–	–	–	–	–	○ ○	+	+	+	...	...	...

Length of life-cycle, egg to adult, here is about $11\frac{1}{2}$ months.

Diagram D.

Exceptional case in length of life-cycle—here brood material was of poor quality and in dense shade.

Year	Jan.	Feb.	March	Apl.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
1916	...	...	...	...	...	...	+ •	• –	–	–	–	–
1917	–	–	–	–	–	–	–	–	...	...	...	...

From the diagrams it will be seen that the length of the larval period is extremely variable. In the typical life-cycle it is from 69 to 71 days, whereas where the beetles hibernate as larvae it may be about $11\frac{1}{2}$ months or longer.

Further, it is obvious that owing to this great variation in the length of the life-cycle there is a great deal of overlapping of generations of beetles.

LENGTH OF LIFE OF *C. ABIETIS* AND THE NUMBER OF GENERATIONS IN A YEAR.

It is now recognised amongst workers on Curculionids and Scolytids that many of these beetles may not only have a long individual life but that the newly issued young brood of beetles cannot proceed at once to an efficient copulation followed by egg-laying. Eichhoff and his school believed the contrary. More recent workers however, including Von Oppen, Nusslin, and MacDougall for Curculionidae, and Pauly, Nusslin and Knocke and Fuchs for Scolytidae, proved that Eichhoff's view was erroneous.

My own recent work[1] on the Scolytids *Myelophilus piniperda* Linn. and *Myelophilus minor* Hart. has corroborated the view of these later workers. From the results of the researches of these workers it has also been definitely proved that a large number of forest insects belonging to the Scolytids and the Curculionids do not die after pairing and a first egg-laying, but that after a period of renewed feeding in order to recuperate and to render their sexual organs once more functional, it is possible for them to proceed to a second pairing and a second egg-laying. Von Oppen and others also showed that the imago on its transformation from the pupal condition might be quite unripe and unable to proceed to an efficient copulation followed by egg-laying, and that in such a case an intervening feeding period was necessary for the reproductive organs to become mature.

Further, the question of whether two broods in the relationship of parents, children, and grandchildren are possible in a year is greatly dependent on two things, viz. whether a preliminary feeding is necessary before breeding and if this feeding period be short or long. If this feeding period be short then a second brood in the year is possible, whereas if the period is long a second brood is impossible.

The proving of the facts is not an easy matter in the case of *C. abietis* where the most of the feeding previous to exit for mating takes place under the bark in the place where the insect has reached its imago stage. As underneath the bark of an infested branch or stem it is possible to find Cryphalus beetles that have already bred and beetles that have just reached the imago stage and have not bred at all, the true facts as to length of life, number of broods possible, and the generations possible in a year can only be ascertained by a dissection and comparison of the reproductive organs of new imagos, beetles ready to pair, beetles that are laying eggs and beetles that have completed egg-laying.

THE MALE REPRODUCTIVE ORGANS OF *CRYPHALUS ABIETIS*.

Fig. 11 shows the male reproductive organs dissected out. These comprise the testes, vasa deferentia, seminal vesicles, accessory glands, common vas deferens or duct and the penis. The testes are translucent glandular bodies and as usual one lies on either side of the abdomen ventrally. These produce the spermatozoa. Each testis (*T.*) is made up of two lobes somewhat circular in shape and closely united along their inner surfaces. From the posterior or under side of each testis, a duct

[1] *Trans. Royal Society Edin.* vol. LII, Part 1, No. 10.

or tube arises known as the vas deferens (*V.d.*). The vasa deferentia unite later to form a common duct (*C.d.*) which leads to the penis. The vas deferens is much swollen but there are constrictions on it at two points. The first constriction occurs at a point distant from the testis of about one-quarter of its total length, while the second is at a point about a corresponding distance from the other end of the vas. The first constriction is most marked, the second is not so conspicuous. The swollen

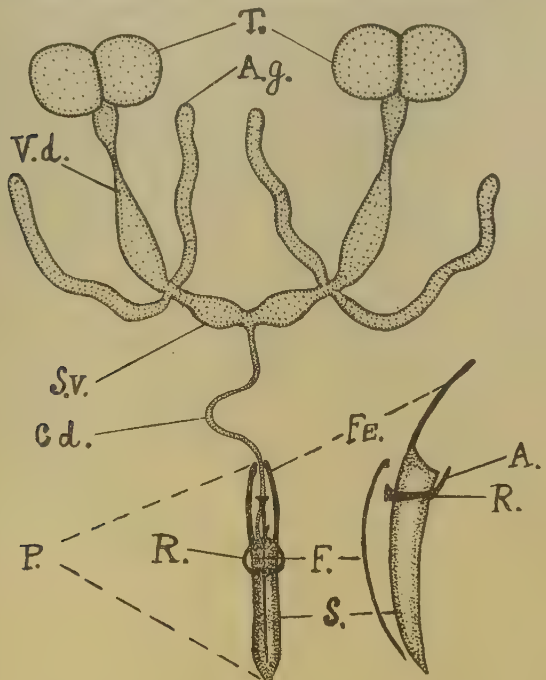

Fig. 11. Male reproductive organs of *C. abietis* (greatly magnified). On the right the penis is shown in side view (more highly magnified).

portion of the vas lying between the second constriction and its union with the vas deferens from the other testis, *i.e.* the most posterior portion of each vas, is called the seminal vesicle (*S.v.*). Two blind diverticula, the accessory glands (*A.g.*), one on either side and placed opposite each other, open into the vas deferens just at its second constriction. The chitinous portion of the penis (*P.*) is composed of the fork (*F.*), ring (*R.*) and sheath (*S.*). The fork gradually tapers to a point while anteriorly

it widens out slightly into a triangular-shaped knob showing very frequently rounded projections on either side. The ring, on the whole, is circular in shape and surrounds the sheath of the penis. In a lateral aspect (Fig. 11) of the chitinous portion of the penis, the dorsal portion of the ring is seen to be drawn out to a point which projects anteriorly. This drawn-out portion of chitin is called by Hopkins[1] the apodemal process (*A.*).

The sheath, roughly speaking, may be considered as a hollow chitinous cylinder tapering posteriorly and bearing on its anterior edge two chitinous rods known as the femora (*Fe.*). In the following columns I contrast the main characters of unripe and ripe reproductive organs of the male, which proved useful to me in differentiating them.

Unripe	Ripe
Testes white.	Testes yellowish.
Vas deferens, *i.e.* portion between testis and seminal vesicle, dirty white in colour.	Vas deferens, *i.e.* portion between testis and seminal vesicle, yellowish in colour.
Seminal vesicle small.	Seminal vesicle swollen.
Accessory glands short and thin, only slightly developed.	Accessory glands greatly lengthened.

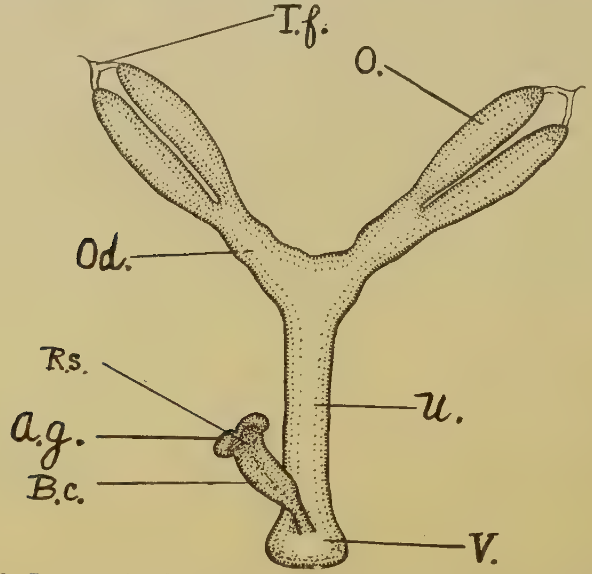

Fig. 12. Immature female reproductive organs of *C. abietis* (greatly magnified).

[1] Hopkins, Preliminary Classification of the Superfamily Scolytoidea, Technical Series, No. 17, Part II, *U.S. Bureau of Entomology*, 1915, p. 193 *et seq.*

FEMALE REPRODUCTIVE ORGANS OF *C. ABIETIS*.

Fig. 13 depicts the reproductive organs of a female about to proceed to egg-laying.

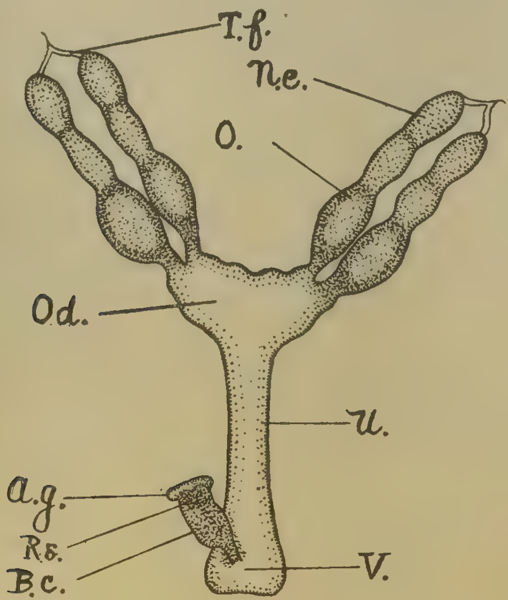

Fig. 13. Reproductive organs of female *C. abietis* about to lay eggs (greatly magnified).

There are two ovaries, one on each side of the abdomen. Each ovary (*O.*) consists of two egg-tubes, which open into the paired oviduct. At the anterior extremities of each egg-tube there is a terminal nutritive chamber (*N.c.*) and at its apex a terminal filament (*T.f.*). The eggs pass from the egg-tubes to the oviducts which unite posteriorly to form a common duct—the uterus (*U.*) and the vagina (*V.*). Uniting with the posterior portion of the uterus we have the bursa copulatrix (*B.c.*) enclosed in the anterior end of which is the receptaculum seminis (spermatheca) (*R.s.*) and bearing anteriorly also the accessory gland (*A.g.*).

Repeated dissections of the reproductive organs of numerous females, both immature and mature, were made with the object of ascertaining definitely whether a slime or a pair of slime glands were present or not, but in all these I failed to observe any trace of them. (Such slime glands are present in the female reproductive organs of many Scolytids and

usually enter the lower portion of the uterus (the vagina) prior to the entrance of the bursa copulatrix.)

According to Nusslin[1] the bursa copulatrix in the genus Cryphalus is obscure or absent. From repeated dissections of the female reproductive organs in all stages of development for the purpose of investigating this point I should say rather that the receptaculum seminis is the obscure portion of the reproductive apparatus, for it is only in the reproductive organs of females that have just completed egg-laying that the position and outline of this part is traceable at all. In all stages of the development of the reproductive organs of the female I have found the bursa copulatrix quite easily discernible but at the same time there is no distinct line of demarcation between it and the receptaculum seminis. In my opinion the bursa copulatrix encloses the receptaculum seminis in its anterior end and this can be a possible reason for its obscurity.

The sequence of changes which I observed to take place in the reproductive organs of the female during their transition from the immature to the mature state and to their condition after egg-laying may be summarised as follows:

In the immature state (Fig. 12) the egg-tubes are colourless and are comparatively uniform throughout their length. The bursa copulatrix is colourless and empty while the receptaculum seminis enclosed within it is scarcely traceable. The accessory gland of the receptaculum is small and inconspicuous.

The first noticeable change in the reproductive organs is the slight narrowing of the lower portion of the egg-tubes while the contents of this portion become muddy coloured. Later some of this muddy coloured substance passes down into the oviduct which now becomes much swollen. Following on this, the egg-tubes, by a shunting-off process which takes place in the middle or posterior portion of each tube, become more elongated. Soon the egg-tubes divide up in bead-like fashion, each bead or egg-chamber containing an egg. In this stage, depicted in Fig. 13, we see that the oviduct is still swollen; the bursa copulatrix is full and is muddy in colour and the receptaculum seminis enclosed in the bursa copulatrix is still obscure. As soon as an egg has passed through the neck or lower portion of the egg-tube (see Fig. 14), this portion contracts, swelling out and contracting again each time an egg passes through it. From Fig. 14 it might seem that an egg is passed into the oviduct first from one ovary then the other in turn.

[1] See Hopkins, p. 195.

Egg-laying being completed the egg-tubes are now empty or contracted as shown in Fig. 15. The oviduct also is contracted while the outline of the receptaculum seminis enclosed in the anterior end of the bursa copulatrix is now traceable.

In the case of females which had completed egg-laying and had fed for a period of about four months prior to a possible second egg-laying, I found that, with the exception of a slight increase in the size of the terminal or nutritive chamber, the parts of their reproductive organs had undergone little further change in appearance.

In all my dissections of the reproductive organs of females both in the egg-laying and after egg-laying stages I failed to notice any trace of the so-called corpora lutea, or heap of degenerate yellowish tissue, which in many insects frequently collects at the bases of the egg-chambers as soon as eggs have passed into the oviduct.

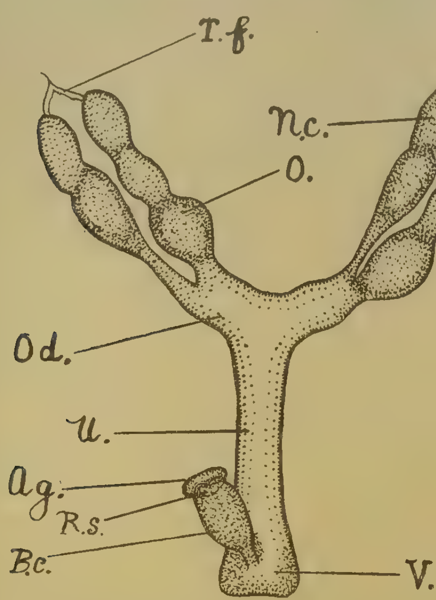

Fig. 14. Reproductive organs of female *C. abietis* egg-laying (greatly magnified).

In the following columns I emphasize the significant characters which appeared to be most useful in determining the unripeness and ripeness of the female reproductive organs.

Unripe	Ripe
The nutritive chamber at the apex of the egg-tubes is small and apparently seated directly on the oviduct.	Nutritive chamber large.
Egg-tubes diminutive, short, not prominent, not separated off into ovarian chambers.	Egg-tubes long and pointed so as to suggest strings of beads. The egg-chambers increase in size gradually from the nutritive chamber to the oviduct.
Bursa copulatrix empty. Gland associated with the receptaculum seminis empty.	Bursa copulatrix and gland associated with receptaculum seminis well filled.

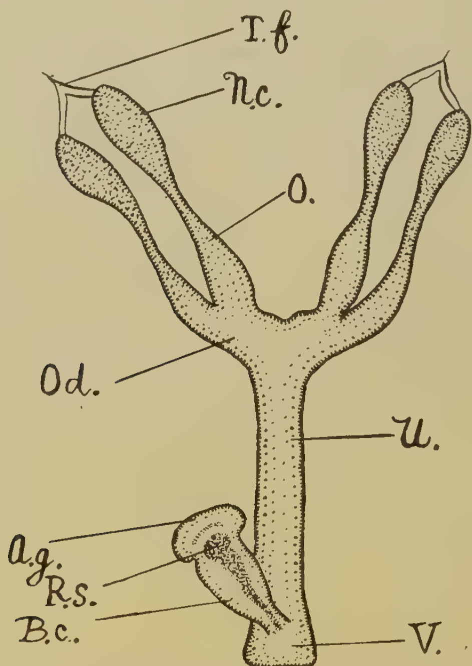

Fig. 15. Reproductive organs of female *C. abietis* after egg-laying (greatly magnified).

QUESTION OF THE NUMBER OF GENERATIONS IN A YEAR.

From repeated observations made in the open and from my experiments I am convinced that even under the most favourable conditions the occurrence of a double generation in the succession of parents, children and grandchildren within a single year is most unlikely.

In Table No. I, I have summarised my observations and results of the control experiments already referred to under the paragraph dealing with the length of a life-cycle in a single generation. From this table it will be seen that the new generation developed from eggs laid in May of the year and issuing in September is unable to proceed to an egg-laying, *i.e.* a new generation, in the same year. At the earliest it would be the next spring before they laid eggs. Similar results were also obtained from experiments and dissections from material bred in the open in the summer and autumn of the year 1917.

Table I.

Date of liberation of adults proceeding to make gallery	Boring mother gallery	Adult stage of new generation reached	Reproductive organs of females dissected out	Results of microscopic examination	Remarks
2 May 1917	4 May 1917	27 Sept. 1917	9 Oct. 1917	Immature	Egg-laying would not take place till following spring as little or no feeding takes place in the months November to March
do.	do.	do.	22 Nov. 1917	do.	
do.	do.	do.	3 Dec. 1917	do.	

Even adults derived from overwintering larvae and which issue in midsummer do not have a new generation in this year as is proved by the undernoted observations.

Some larvae that hibernated during the winter of 1916–17, the first of which pupated on June 5th, 1917, issued as adults from July 21st, 1917, to August 20th, 1917. The majority of these young adults however never swarmed at all during the year 1917 but remained underneath the bark where they were reared and hibernated the second winter as immature adults. That they were immature was proved from a large series of dissections made of their reproductive organs in November and December, 1917.

Some of the reproductive organs of those adults that did swarm in July and August of 1917 were also examined as the beetles issued from the material where they had been reared but they too were found to be immature. The others that issued I liberated on August 14th, 1917, in muslin cages enclosed within which were paraffined branches of Silver Fir, on which they could feed or breed as they chose. On the 16th of August, 1917, a number of them were found to be boring on the Silver Fir branches, evidently feeding. Examination of these branches was made at intervals up to Dec. 3rd, 1917, but in no case were eggs found in any of their

borings. This is remarkable as a number of males and females were working together. The dissection of the reproductive organs of a number of these beetles on November 29th, 1917, and up to December 3rd, 1917, however showed that although they had been feeding for some time the reproductive organs were not ready for egg-laying.

ARE TWO BROODS IN THE RELATIONSHIP OF BROTHERS AND SISTERS POSSIBLE IN A YEAR?

My observations show that when the parent beetles have bred and their brood gallery is completed sometimes the male dies before the female has laid her last egg, the female beetle surviving. Very frequently the females die immediately after laying is completed and in many cases the males survive. In some cases both parents die, in others both survive after a first breeding. The mortality amongst parents that have already bred is considerable. Those survivors, male or female, tunnel galleries of a much similar appearance to those of the larval ones and feed on the gnawed material, obtaining nourishment from it and so recuperate their reproductive organs for a possible second egg-laying.

In my experiments a number of parent beetles that had completed egg-laying in the end of June, 1917, tunnelled and fed. The results of these experiments are shown in Table II.

TABLE II.

Date of completion of 1st egg-laying	Found feeding in pseudo-larval galleries after 1st egg-laying	Reproductive organs of females dissected out	Result of microscopic examination	Remarks
26 June 1917 approx.	2 July–20 Nov. 1917	20 Nov. 1917	Immature	A 2nd egg-laying would not take place if at all till following spring.
do.	do.	27 Nov. 1917	do.	
do.	do.	3 Dec. 1917	do.	
do.	do.	10 Dec. 1917	do.	

HOST TREES.

From observations made in the field I find that *C. abietis* confines itself in Scotland to breeding on the stems, branches and twigs of unhealthy, dying, or dead trees of three closely allied genera of conifers, namely, Abies, Picea, and Pseudotsuga. Like many other injurious insects *C. abietis* has a preference for certain genera and species, but if these are found wanting, deficient or in an unsuitable state for brood purposes others may be chosen.

My experience in Aberdeenshire, Kincardineshire and Midlothian leaves me with no doubt that *C. abietis* prefers, in Scotland at least, the

genus Abies (Silver Fir family) for brood purposes, having a special preference for the species *Abies pectinata* D.C. (Common Silver Fir). I have also found Cryphalus breeding on *Abies cephalonica* Link. (Grecian Silver Fir) while in my breeding experiments the same insect readily took to *Abies nordmanniana* Spach. (Norman's Silver Fir), and *Abies pinsapo* Boissier (Spanish Silver Fir). It has also been recorded in Scotland on *Abies nobilis* Lindl., a North American species. It is possible that all the species of the genus Abies may be used for brooding purposes if in a suitable condition.

Next in order of preference, *C. abietis* takes the genus Picea (Spruce family), *Picea excelsa* Link. or Norway Spruce being the host plant on which I have found it.

Last in order but by no means of least importance *C. abietis* may choose for brood purposes the genus Pseudotsuga (Douglas Fir family). I have found the insect breeding freely in Aberdeenshire on the sickly branches of standing Douglas Firs, *Pseudotsuga Douglasii* Carr., the only species of the genus planted in this country.

We see then that *C. abietis* possesses a wide range of host trees, an exceedingly important factor which would have to be reckoned with in dealing with the control of the species.

As far as my observations go I am convinced that *C. abietis* in most cases only takes to the Spruce and Douglas Fir families when the preferred Silver Fir family is deficient or is in an unsuitable state for brooding purposes.

On the continent of Europe, according to Nusslin[1] and other writers, *C. abietis* is typically a Spruce species. Nusslin also states that, although it prefers the species of the genus Picea it also takes the genus Abies and occasionally the genus Pinus. Of the species of the genus Pinus he states that it prefers *Pinus strobus* L. or Weymouth pine.

Kaltenbach[2] quoting Ratzeburg names the species as attacking *Pinus strobus* and the dry branches of Silver Fir. Eichhoff[3] names as host plants Spruce, Silver Fir and Pine.

ECONOMIC IMPORTANCE OF *C. ABIETIS* IN SCOTTISH FORESTRY.

Occasional references in the forest literature of Central Europe indicate that *C. abietis* has been known to be harmful especially if in numbers it attacked very young stems.

[1] Nusslin, *Leitfaden der Forst Insektenkunde*, 1905, pp. 201–2.
[2] *Die Pflanzen-Feinde aus der Classe der Insekten*, p. 685.
[3] *Die Europaischen Borkenkafer*, by W. Eichhoff, p. 177.

So far as my observations in Scotland show, *C. abietis* has not proved of any great forest importance in the sense of having proved destructive to live trees, but the species must not be overlooked or observation on it neglected.

A knowledge therefore of its habits as well as the recognition of the presence of the beetle in our woods at the present time is opportune.

Its favourite breeding places are dead or almost dead trees, twigs and branches, of practically all ages, that have been spoiled or killed by some agency or other such as wind, breakage, etc. The positions most commonly chosen by the parent beetles for tunnelling their brood galleries are around twigs and branches, the female commencing her gallery in the axil of a side branch. No doubt she chooses this position because a good foothold is secured for her while boring the entrance hole of the gallery. Boring gradually round the base of the side branch she cuts the inner bark layers, namely the bast and cambium, leaving only the thin layer of outer bark. Where the twig or branch around which she has excavated her burrow or gallery is a small one it may be completely girdled and isolated from the main branch. Even when the twig or branch is strong and although only partially girdled by one gallery it may be completely girdled and isolated from the main branch or stem by other galleries. Were such workings then to be cut on living twigs and branches it is quite evident that serious damage would be done to trees, for no food material from these isolated portions could pass down to the main stem and roots.

A point worthy of mention in connection with *C. abietis* is that it is negatively heliotropic, the parent beetles preferring bushy twigs and branches in shady places unexposed to the sun. For example, the topmost branches of heaps of brushwood lying in the open are not commonly chosen for brood purposes, while the lower branches of such heaps as well as entire heaps in the shade of standing trees may be badly infested. Most likely those branches which are exposed to the sun are too dry for breeding on and this can be a reason why they are not chosen by the parent beetles.

To ascertain if beetles are present in a wood one has only to examine carefully the axil of a dead twig or branch, when, if beetles are at work, a minute heap of fine bore dust, reddish yellow in colour, will be seen. If a number of beetles have issued a series of minute exit holes may be seen at irregular intervals on the surface of the bark. Frequently one will find on examination of branches where the majority of the beetles

have issued that the outer bark layer is broken and the wood surface exposed to view.

NATURAL ENEMIES OF *C. ABIETIS.*

From observations made in the field during the last two years I am of the opinion that the bark fungi play little or no part in controlling the numbers of *C. abietis*. Only on a few occasions have I found beetles killed by fungoid attack.

The larvae are destroyed in numbers by the larvae of a Hymenopterous parasite belonging to the family Chalcididae. On the removal of a piece of the outer bark layer of a badly infested branch or twig one repeatedly met this parasite either in the larval or pupal stage. Only one parasitic larva was found on each host. No cocoon is spun by this Chalcid larva prior to pupation but the pupa lies naked in the Cryphalus gallery or pupal bed. As soon as these parasites have reached the adult stage each gnaws a minute puncture through the outer bark and escapes into the open.

From some Silver Fir branches badly infested with *C. abietis* which I collected in Aberdeenshire in October, 1916, large numbers of these Chalcids issued from July 21st to August 6th, 1917, just at a period when large numbers of these *C. abietis* larvae would be found on infested branches.

The number of these Chalcids varied to a great extent in different localities. From one lot of badly infested material collected in one particular area in the Aboyne district only a few parasites issued. On the other hand, from badly infested material collected from another area a little over a mile from the first exceedingly large numbers of parasites issued. In a single day as many as 30–40 individuals escaped from a few pieces of badly infested material. In this particular case I estimate about 75 per cent. of the larvae of the beetles must have been destroyed.

The abnormal conditions prevailing in our forest areas during the past three years have undoubtedly been the means of creating an excessive number of breeding places for our bark-boring beetles. Foresters throughout the country ought therefore to be on the alert. The intensive study of the life-history and habits of this beetle and of other such forms is for this reason of more than usual interest at the present time.

In conclusion my thanks are due to Dr R. Stewart MacDougall for the encouragement and facilities he has given me throughout this work.

A COPPER EMULSION AS A FUNGICIDE.

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(With Plate XI.)

In the report of the Agricultural and Horticultural Research Station, Long Ashton, for 1917, A. H. Lees described methods of preparing an emulsion containing copper by mixing a solution of copper sulphate with soap solutions.

In conjunction with other experiments, a very similar emulsion was made and used at Wye early in 1917. Since the observations made at Wye as to the nature of this emulsion corroborate those of Mr Lees, and since additionally the fungicidal properties of this emulsion have been examined, it seems desirable to record the work so far done, although further experiments must be carried out before an emulsion of this kind can be recommended as a practical spray fluid.

The emulsion prepared at Wye contained rather more copper than that made by Mr Lees. It contained the equivalent of 0·4 per cent. copper sulphate ($CuSO_4 . 5H_2O$) and 2 per cent. of soft soap[1] and was made by pouring slowly a 0·8 per cent. solution of copper sulphate into an equal volume of 4 per cent. soft soap solution, stirring well all the time. The emulsion made in this way did not settle, even on standing for several weeks; it could not be filtered and turned chocolate colour on addition of potassium ferrocyanide. When the soap solution was added to the copper solution a quite different result was obtained, and instead of an emulsion (probably of copper stearate in part) green sticky masses having a putty-like consistency were formed.

In order to determine whether the emulsion made as above described possessed fungicidal properties, the following experiment was carried out on August 8, 1917.

Fresh potato shoots were brought into the laboratory, cut under water and placed with ends in water in flasks the mouths of which were under water. On each of two shoots, three leaves at successive nodes were

[1] The soap used throughout these experiments is that sold under the name of "Chiswick Soft Soap."

selected; the uppermost and lowest leaves were sprayed with freshly made copper emulsion by means of an atomiser and the middle leaf left unsprayed. When the sprayed leaves were dry, drops of distilled water containing motile zoospores of *Phytophthora infestans* were placed on all three leaves by means of a platinum loop, two drops being placed on each side of the midrib of the lower side of the terminal leaflet and the second pair of leaflets in each case. The zoospores were obtained by placing affected leaves with ends in water under a bell jar on the previous day and leaving overnight. From one to two hours before the zoospores were required, the portions of the leaves bearing sporangiophores were brought in contact with a few drops of distilled water in a watch glass; numerous sporangia became free in the water and zoospores were liberated within an hour.

Three days later, on August 11, there were black spots on both unsprayed leaves but none on any of the sprayed leaves. On August 13, one of the sprayed inoculated leaves had fallen off so the observations were not continued.

On August 15, a second experiment was carried out on growing potato plants in the garden. Three healthy leaves were selected on successive nodes; two of these, the uppermost and lowest, were sprayed with freshly made emulsion and the other left unsprayed. About two hours after the leaves had been sprayed, there was a heavy thunderstorm lasting about ten minutes, so the leaves were not inoculated until the next morning. These were inoculated in the way described in the previous experiment.

On August 20, the unsprayed leaf showed seven distinct diseased spots though there were no spots on either of the sprayed leaves and on September 11, when the whole of the unsprayed leaf was destroyed, the whole of one of the sprayed leaves was quite uninjured; on the other sprayed leaf, one leaflet, though not one of those inoculated, was withered but otherwise the leaf was quite green and uninjured. On this date, the shoot was removed from the plant and photographed (see figure).

The two lowest leaves shown in the photograph had become naturally infected; the two healthy leaves seen on the right had been sprayed with the emulsion and then inoculated, and the diseased leaf occurring between the two healthy ones had been left unsprayed but had been inoculated.

The accompanying table shows in detail the observations made on the inoculated leaflets.

Detailed observations of Experiment II.

Inoculated August 16		August 20	August 23	August 28	Sept. 11
Leaf *a* sprayed	terminal leaflet	no diseased spots	no diseased spots	no diseased spots	Whole leaf uninjured
	left ,,	do. do.	do. do.	do. do.	
	right ,,	do. do.	do. do.	do. do.	
Leaf *b* unsprayed	terminal ,,	1 distinct spot of blight	1 spot 1 cm., another 0·3 cm. diam.	All three leaflets destroyed	Whole leaf destroyed
	left ,,	2 distinct spots of blight	The two spots have coalesced		
	right ,,	4 distinct spots of blight	Whole leaflet blackened and withered		
Leaf *c* sprayed	terminal ,,	no diseased spots	no diseased spots	no spots	no spots
	left ,,	do. do.	do. do.	do.	do.
	right ,,	do. do.	do. do.	do.	do.

On the same date as the last experiment, a plant with many badly diseased leaves was sprayed with the emulsion but the disease extended in all the affected leaflets.

From these experiments, it is evident that the emulsion acted as a preventive against infection by zoospores of *Phytophthora infestans* and justified trials on a larger scale.

Later in the year, two small plots of potatoes, each measuring approximately 120 sq. yds, were sprayed with the emulsion and on this occasion when tap water was used instead of distilled water hitherto employed in these experiments, a little difficulty was experienced in spraying the fluid owing to the accumulation in the nozzles of the sprayer of the green sticky substance referred to already.

At the time the crop was lifted the leaves of the sprayed plots were certainly much greener and showed far less damage by blight than those of the unsprayed control plot, but owing to the lateness of the appearance of the blight, all three plots had approximately the same low percentage of diseased tubers although the two sprayed plots showed a slightly greater total yield than the control plot.

In 1918, these trials were repeated and two more small plots, each approximately 36 sq. yds in area, were sprayed, the control plot of the same size being between them. On Plot I, the emulsion described (*i.e.* containing the equivalent of 0·4 per cent. $CuSO_4 . 5H_2O$ and 2 per cent. soft soap) was sprayed. On Plot III, an emulsion containing twice as much copper and twice as much soap was used. The plots were sprayed on August 7. Each plot received six gallons, applied by means

of a knapsack sprayer, and both emulsions were made with rain water and were applied in the usual way by a man accustomed to the work, but no unusual care was taken to effect complete treatment of the plot.

To make six gallons of emulsion for Plot I, three gallons of soap solution containing 1·2 lbs. (544·3 gms.) of soap were put in a perfectly clean wooden pail; 0·24 lb. (108·9 gms.) of copper sulphate was dissolved in three gallons of water and this solution was added slowly to the soap solution, which was stirred well all the time.

On August 19, both plots were sprayed again, each receiving six gallons as before. On this occasion both emulsions were made with tap water and Plot I was actually sprayed with emulsion made from tap water though a small amount of a putty-like substance was formed; this remained in the strainer and the whole of the spray went on satisfactorily. In the case of the stronger emulsion, a mass of green "putty" was formed, clogging up the tube and nozzles of the sprayer, even after straining, which was a very long process; this was therefore rejected, the sprayer thoroughly cleaned and the emulsion made again with rain water. Although some "putty" was formed, the emulsion which was put on Plot III contained considerably more copper than that put on Plot I.

The green putty-like substance has strongly adhesive properties and some method has yet to be found for retaining all the copper in the emulsified condition.

The effect of the spray on the leaves was most striking. The control plot began to blacken about three weeks before the sprayed plot showed any signs of being affected and on September 25, when the sprayed plots were still fairly green and healthy, not one green leaf could be seen on the control plot.

From the results given, it will be seen that the sprayed plots gave an appreciably higher yield than the unsprayed and the percentage of diseased tubers was much higher in the unsprayed plot than in either of the sprayed plots.

Plot I. Sprayed twice with an emulsion containing approximately the equivalent of 0·4 per cent. $CuSO_4 . 5H_2O$.

		%
Ware	63 lbs.	70·8
Chats	18½ ,,	20·8
Blight	7½ ,,	8·4
Total	89 ,,	

Plot II. Unsprayed.

		%
Ware	34 lbs.	61·8
Chats	13 ,,	23·6
Blight	8 ,,	14·5
Total	55 ,,	

Plot III. Sprayed twice with emulsion containing approximately the equivalent of 0·8 per cent. $CuSO_4 . 5H_2O$.

		%
Ware	72½ lbs.	81·9
Chats	13 ,,	14·7
Blight	3 ,,	3·4
Total	88½ ,,	

From these experiments, it would appear that the copper emulsion at the lower strength (containing the equivalent of 0·4 per cent. $CuSO_4 . 5H_2O$ and 2 per cent. soft soap) is an efficient preventive against blight when used on potato foliage, and when carefully prepared with rain water it can be applied without difficulty. Further experiments, however, are necessary, particularly with respect to its preparation when only hard water is available, before it can be generally recommended as a practical spray fluid. Although this fluid was originally prepared and examined from another point of view, on account of the small amount of copper used in its preparation and of its fungicidal value, it is worth while trying to overcome the difficulty experienced in making the emulsion under practical conditions. From an economic point of view, the large amount of soap required is partly compensated for by the small amount of copper necessary and the property of spreading over the foliage which soap gives to the fluid.

The fungicidal value of the emulsion, which contains much less copper than Burgundy or Bordeaux mixtures as commonly used, is probably due, in part, to the fact that the particles, owing to their extreme fineness, must come in intimate contact with the leaf surface and to the adhesive nature of the copper compound which it contains.

Summary. An emulsion containing the equivalent of 0·4 per cent. copper sulphate ($CuSO_4 . 5H_2O$) can be made by mixing solutions of copper sulphate and soft soap, and this exhibits preventive action against the attacks of the potato blight fungus.

In conclusion, we should like to thank Dr Eyre, who indicated the possibility of preparing an emulsion by the method adopted, and at whose suggestion the above experiments were carried out.

DESCRIPTION OF PLATE XI

Photograph of potato shoot described on p. 201. The two healthy leaves seen on the right had been sprayed with copper emulsion and then inoculated with zoospores of *Phytophthora infestans*; the diseased leaf occurring between these had been left unsprayed and had been inoculated. The remaining leaves on the shoot had become naturally infected.

STUDIES IN BACTERIOSIS II[1].

A BROWN BLOTCH DISEASE OF CULTIVATED MUSHROOMS.

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INTRODUCTION.

During the spring of 1918 a disease of mushrooms was observed in the beds of a large nursery in Brentford, Middlesex. Mushrooms have been cultivated there for upwards of forty years, and although the disease was not entirely new to the grower there would seem to have been no outbreak in the past of comparable severity. Previous occurrences had been of little importance and had been attributed to the effect of draughts. The disease was first noticed in April, and threatened to assume serious proportions. On examination of one of the houses in the first week of May about one-third of the crop in certain parts of the house was found to be affected[2]. The financial loss at this time when the wholesale price of mushrooms was at its maximum must have been considerable, affected mushrooms being so disfigured as to be unsaleable. Later on in the month, however, the disease became less prevalent, and towards the end of June had become insignificant in amount. The reason for this rapid falling off will be discussed later.

The Symptoms of the Disease.

Circular or irregular spots of a chestnut brown colour appear on the surface of the cap of the mushroom when this has attained a diameter of an inch or so; they spread rapidly and coalesce to form large patches which occasionally cover the entire surface of the pileus. (See Fig. 1.) The stalks also may show the disease, but it is characteristically a disease

[1] The first of this series of studies appears in *The Journal of Agricultural Science*, vol. VIII, 1917.

[2] The areas most affected were those within ten feet of either door; this seemed to indicate that draughts were in some way connected with the spread of the disease.

of the cap. The patches become slightly depressed, dry up and crack radially as the mushroom grows. They arise at or near the margin of the mushroom or at the point of contact of one with another, *i.e.* places at which water is likely to remain for some time after the sprinkling of the bed. At the outset it seemed likely that some micro-organism finds entrance at these spots after multiplying in such standing water. The disease spreads rapidly from one diseased head to others in the same

Fig. 1. Mushrooms naturally infected.

cluster in a way which supports the above view as to the mode of dissemination of the disease, the organism presumably being carried by insects or by splashings from infected drops of water during watering.

The disease is very superficial; on peeling off the "skin" the underlying tissue is found to be affected to a depth of, at most, one to three millimetres (the diagrammatic sketch, Fig. 3, shows clearly the slight extent of penetration of the tissue by bacteria, in this case less than half a millimetre), and very frequently is found to be perfectly white and healthy. The affected underlying tissue has a rather water-soaked appearance and a mouse grey or yellowish grey colour.

Isolation of the Causal Organism.

Microscopical examination of a section of the grey tissue underlying the brown spot shows that the hyphae are invaded by crowds of bacteria. The preparation from which Figs. 3 and 4 are taken shows the pileus completely disorganised and penetration of bacteria to a depth of about half a millimetre; the organisms are mainly within the cells of the hyphae as is shown in Fig. 4.

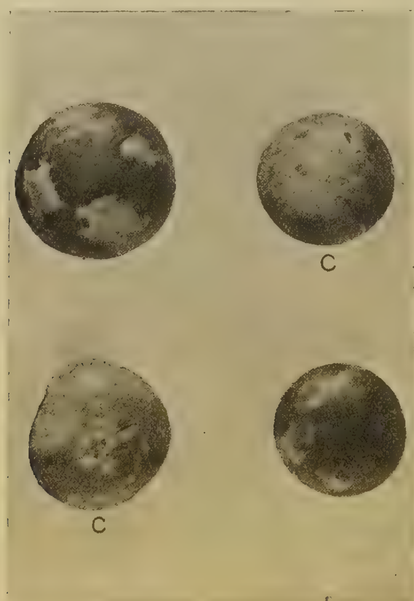

Fig. 2. Mushrooms artificially infected. *cc* controls.

Removal with aseptic precautions of some of the bacterial tissue and inoculation into mushroom-extract or other nutrient media yielded, without the slightest difficulty, pure cultures of an organism which was identical in every case, leaving no doubt that the causal organism had been obtained. The organism was plated several times on mushroom-extract agar and on bouillon-agar in order to ensure purity and from the first the colonies were all of one type.

INFECTION EXPERIMENTS.

Numerous infection experiments have been made upon young mushrooms growing in the beds at Brentford and upon mushrooms removed from the bed and kept in fresh condition with their stalks embedded in moist soil covered with bell-jars. A suspension in sterilised mushroom-

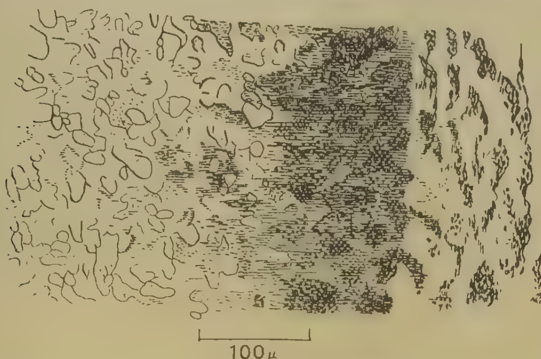

Fig. 3. Camera drawing from a 3μ radial section through the cap of a diseased mushroom, showing complete disorganisation of the outer hyphae and penetration of the tissue by bacteria to a depth of not more than half a millimetre.

Fig. 4. Camera drawing from same section as Fig. 3, showing hyphae penetrated by bacteria.

extract of the organism from an agar slope was painted over the surface of the mushroom with a sterilised camel-hair brush, numerous control experiments with the uninoculated extract being made at the same time. In every case typical brown streaks corresponding closely to and spreading irregularly from the margins of the pattern painted resulted from such inoculations. (See Fig. 2.) The controls showed either no sign at all, or a slight indentation caused by the mechanical injury of the soft tissue of the mushroom. The infections at Brentford were examined only after three days, but in those made in the laboratory the pattern was well developed overnight and did not extend far afterwards. In some of these the browning was distinctly visible in as short a time as five hours; this led to the suspicion that ammonia might be the direct cause of the browning, and that the organism invading the hyphae was one of the common ammonifiers of the soil which had entered dead tissue resulting from the lethal action of ammonia upon the cells, a mode of entry of a saprophyte into a living plant which the work of Jensen (4) has shown to be possible.

To test this hypothesis control experiments were made with mushroom-broth containing additions of ammonia; when these additions were quite small, sufficient only to render the broth just alkaline to litmus, no coloration whatever was produced, but with addition sufficient to make the liquid smell distinctly of ammonia a brown coloration was obtained but of a dull tint easily distinguishable from the warm chestnut shade characteristic of the disease. Further control experiments were made with suspensions of *Bacillus fluorescens liquefaciens*, *Bacillus Proteus*, and *Bacillus mesentericus*, all of which are powerful ammonifying organisms of the soil, and, although repeated on many occasions with cultures of various ages, no browning of the tissue resulted.

The organism was, then, to be regarded as a parasite and this was later definitely established by the loss of virulence in some agar cultures of two months' standing, and in sub-cultures of 24 hours' growth made from these.

DESCRIPTION OF THE ORGANISM.

I. Morphological Characters.

Form and Size. The organism is a short rod with rounded ends. In common with most others it varies considerably in size, according to the rate of growth and the medium employed. Measurements are held by the author to be of little significance, but for the purpose of comparison, measurements were made upon a 24 hours' growth on bouillon-

agar, the sixth transfer from the original, incubated at 22° C. The colony had attained a diameter of 4 mm. The film was fixed by ten minutes' immersion in 4 per cent. formalin, stained for ten minutes in aqueous methyl violet, and examined in oil. The length of the organism varied from $0 \cdot 9\,\mu$ to $1 \cdot 7\,\mu$ and the breadth from $0 \cdot 4\,\mu$ to $0 \cdot 5\,\mu$. The growth was very viscous and suggested the presence of a capsule; when a suspension of the organism in normal saline was examined by dark-ground illumination, however, no sign of a capsule was discovered.

Motility and Flagella. The organism is actively motile in young cultures in broth and upon agar, but it comes to rest early, frequently after 24 hours at air temperature on solid media. The movement is of a free swimming type without other specific characteristic. The flagella have been stained by Stevens' modification of Van Ermengen's stain and by a new method devised by the late Professor H. G. Plimmer[1]. The flagella are two to four times the length of the organism, one or two in number, occasionally three and more rarely four or five, arranged at one pole. (See Fig. 5.) The organism is therefore a *Pseudomonas*.

Fig. 5. Camera drawing from a preparation stained by the method of Plimmer.

Staining. The organism stains well with carbol fuchsin, gentian violet and methyl violet, does not stain by Gram's method, is not acid fast, and gives negative results with the usual capsule stains.

[1] I hope with Dr R. H. A. Plimmer's permission to publish a description of this staining method if the details can be worked out from the data left by Professor Plimmer.

II. Cultural Characters.

The organism grows equally well in mushroom-extract and in beef-extract (Jardox) bouillon + 10, and on solid media from these. It also grows luxuriantly upon potato-mush agar.

Bouillon + 10. Turbidity was strongly marked after 24 hours at 22° C. A strong pellicle and faint fluorescence were formed in cultures made during the first two weeks after isolation, but both these characters disappeared in later cultures. The pellicle was easily broken by shaking and did not re-form. A strong pellicle also formed on mushroom-extract. In all cases a slight ring was formed, and after a week or so the liquid was very viscous and mucus-like. It had become strongly alkaline to litmus and smelt of ammonia.

Bouillon-gelatine Stab. After 48 hours at air temperature liquefaction had commenced, the top 3 mm. being completely liquid with a funnel-shaped depression extending to a depth of some 10 mm. The bottom of the funnel was occupied by a yellowish white granular mass. Growth along the stab was barely perceptible. Complete liquefaction occurred in about 10 days, at air temperature.

Bouillon-gelatine Plate. After 24 hours at 22° C. the colonies had a diameter of 5 or 6 mm. and liquefaction was basin-shaped with a granular deposit at the bottom. In three days the gelatine was completely liquid with a strong ammoniacal odour, resembling somewhat that of stale urine.

Bouillon-agar Stab. After 24 hours at 22° C. surface growth was yellowish white and about 4 mm. in diameter. Growth along the stab was perceptible only in the top half centimetre. After 72 hours growth could still be seen only towards the top of the stab. The tube was left in the incubator from June 5th till October 2nd, and growth to the bottom of the stab could then be observed, but only by the use of a strong light. The organism was still viable after four months' incubation at 22° C.

Bouillon-agar Slope. The streak was well developed after 20 hours at 22° C. as a dirty bluish-white wet-shining streak 2 mm. wide, with slightly raised flat contour. When collected in mass by a wire the colour was faintly yellow tinted. The surrounding medium was bluish-green but without fluorescence.

Bouillon-agar Slope under Anaërobic Conditions. Growth was slight but distinctly perceptible. The organism is a facultative anaërobe with a very marked preference for aërobic conditions.

Bouillon-agar Plate. Growth was very rapid at air temperature. After 20 hours colonies had a diameter of 1 mm., and after 49 hours of 4 or 5 mm. The colonies were round, raised, wet-shining, and of a dirty greenish-white colour, the margins later became lobed and spreading. There was no fluorescence but a greenish precipitate was formed in the gel surrounding the colonies. Colonies in the depth of the medium were broadly lenticular.

Optimum Temperature for Growth. Tubes of bouillon were inoculated each with one loopful from a broth culture and incubated at 6°, 13°, 18°, 20°, 22°, 25°, and 30° C. After two days' incubation clouding was most dense at 25° C.; growth at 6° C. was not apparent until the fifth day.

Thermal Death Point. Tubes of bouillon were seeded each with 1 cc. of a 24 hours' culture at 25° C. They were immersed in a bath at the usual range of temperatures, the temperature of the tubes being controlled by a thermometer immersed in a control tube of broth. Ten minutes heating was allowed at each of the temperatures given below and the tubes were then incubated at 25° C. for seven days.

Temperature of bath	Temperature of control tube	Result
46°	45° rising to 46°	Living
48°	46° ,, 48°	,,
49°	47° ,, 49°	,,
49·5°	48° ,, 49·5°	,,
51°	50° ,, 51°	Dead
52°	51° ,, 52°	,,

III. Physiological Characters.

The culture used for these experiments was the fifth transfer from the original and had been on no other medium than bouillon-agar + 10. A tube of bouillon was heavily inoculated and a loopful from this used for each test. The temperature of incubation was 22° C.

10 *per cent. Witte Peptone* + 1 *per cent. Glucose.* Acid on the second day, no gas formed in Durham tube; no change after 15 days.

10 *per cent. Witte Peptone* + 1 *per cent. Lactose.* No acid and no gas; a thin film with an oily appearance, a slight ring formed and liquid became slightly turbid.

10 *per cent. Witte Peptone* + 1 *per cent. Saccharose.* No acid and no gas; growth as above.

Bouillon + 2 *per cent. Glucose.* Acid after 24 hours, no gas, no pellicle, no ring; no further change up to 15 days.

Bouillon + 2 *per cent. Lactose.* No acid, no gas, slight pellicle, no ring.

Bouillon + 2 *per cent. Saccharose.* No acid, no gas, slight pellicle, no ring.

Bouillon + 2 *per cent. Mannite.* No acid, no gas, no pellicle, no ring; slightly bleached at bottom of tube after 15 days.

Uschinsky's Solution. Alkaline on second day, no gas, loose pellicle, no fluorescence. After 15 days: completely bleached, no gas, no fluorescence, thin pellicle and strong ring. After two months: blue above, bleached below, no fluorescence, very viscous deposit. After four months: the ultramarine colour had completely returned.

Litmus Milk. Curd separated after the fourth day, the reaction was neutral but became slightly alkaline later. On the seventh day the curd occupied only one-third of the volume of liquid, the litmus was bleached and a strong green fluorescence developed in the whey. Most of the curd was digested but some remained at the bottom of the tube after six weeks.

Milk. The curd formed and was partially digested as above, and the whey became strongly fluorescent.

Potato Plug. After two days the streak was visible as a white, wet-shining, raised mass; after five days the colour had assumed a faint yellow tinge; the potato was not discoloured. Pulped in water after three weeks, the iodine test showed slight diastatic action.

Dunham's Solution. Became slightly turbid on the second day; no pellicle and no ring formed. After 30 days a trace of indol was present.

Nitrate Bouillon. A loose pellicle formed after 24 hours, the liquid became very viscous and of a yellowish-green colour. Nitrate was not produced, but ammonia was formed. This was probably a product of the breakdown of protein since nitrate was still present after two months' incubation. The presence of nitrate was not due to the death of the organism previous to destruction of all the nitrate since the culture was found to be still viable at the end of two months. No gas was formed.

GENERAL DISCUSSION, COMPARISON OF THE ORGANISM WITH ALLIED STRAINS.

In searching for the mode of entry of the organism to the sheds the possible sources to be considered were: (1) the manure used in making the beds; (2) the spawn; (3) the mould used for casing; (4) the straw litter for covering the beds after spawning; (5) the water used for sprinkling; and (6) the air. Suspicion of the manure was removed by

the fact that during fermentation the temperature usually rises to 120° or 130° F., a moist temperature sufficiently near to the thermal death point of the organism to eliminate this source. The other materials used on the bed, though not free from suspicion, were hardly likely to have introduced the organism, since, as stated in the Introduction, the disease did not appear uniformly distributed over the beds. The water used for sprinkling the beds was deemed to be a likely source. This was taken from the town main and from an old well. Both of these supplies were sampled on two occasions and platings made upon mushroom-extract agar, many colonies of ammonifying organisms developed on the plates and most of these were tested by inoculation upon growing mushrooms, but in no case was there any production of the disease symptoms. Early suspicion fell upon the air as the carrier of the organism since, as stated in the footnote on p. 206, the disease, originating near the doors and windows of the sheds, seemed to be associated with draughts. The litter when removed from the beds was dumped down outside the sheds and some was packed at the bottom of the doors to exclude draught as much as possible; dust from this litter would be carried into the shed each time the door was opened. A search for the organism upon this material, however, proved abortive.

The disease commenced to decrease in early June, and towards the end of June had practically ceased to exist. This may have been, and probably was, in large measure due to the rapid growth of mushrooms during this warm period, the organism, though a tremendously vigorous grower at air temperature, presumably not being able to keep pace with its active host. Another interpretation is, however, possible; the onset of the disease in March and its fall in June, coupled with the fact that the sheds were surrounded by fruit trees in a large orchard, drew the author's attention to the synchronising of the disease with the period of fruit-blossoming, and suggested that the cause of the disease might be identical with that of the "Pear-blossom Blight," investigated by Barker and Grove (1) in this country, and by Doidge (2) in S. Africa.

This disease had not been specially noticed by the grower but practically no fruit set this year and the disease might well have been partially responsible for this failure.

Comparison was therefore made of the morphological and physiological characters of the mushroom organism with the published records of those of the Pear Blight organism (1, 2 and 3). In most of these the two organisms seemed to be identical. Through the courtesy of Professor Barker, a culture of the latter organism was obtained and careful com-

parative experiments were made. The table given below shows how closely the two organisms agree in their physiological behaviour; certain morphological and cultural characters, however, point to differences which although they may not be specific differences at least serve to differentiate the two organisms as separate strains; these characters were constantly observed even after the two had been cultivated simultaneously through a succession of transfers during two months over which the experiments were made. Barker and Grove's organism does not grow so rapidly as the mushroom organism, it forms long thread-like involution-forms on the second day at 25° C. which the latter does not, it has its optimum for growth at 18° C. whereas the latter grows best at 25° C., the thermal death point which may be conceived to be one of the most secure of criteria is two degrees lower than that of the mushroom organism. Finally, a marked difference is found in the viscosity of liquid cultures: Barker's organism produces in bouillon and Uschinsky's solution[1] a gelatinous deposit in old cultures, whereas the whole solution becomes mucus-like in three-day-old cultures of the mushroom organism.

The organism described by Miss Doidge (2) as the cause of Pear-blossom Blight in S. Africa and named *Bacterium nectarophilum* has many characters in common with the mushroom disease organism. It differs only in the length and number of its flagella, both of which may be merely cultural variations, in the possession of a capsule and in its inability to liquefy gelatine. This last is a very striking character, but we have not as yet sufficient evidence to be able to judge in how far it is a constant one. The work of Morse (5) has shown that in one case, namely that of *Bacillus solanisaprus*, the power to liquefy gelatine could be developed under suitable cultural conditions and that this organism was really a strain of a vigorous liquefier, *Bacillus atrosepticus*. The identity of *Bacterium nectarophilum* with the organism described in this paper is then not beyond the region of possibility, and the hypothesis that Pear-blossom Blight and the Mushroom Disease may be produced by one and the same organism may yet prove to have some foundation in fact. Barker's organism was used in inoculation of mushrooms and found to have no effect upon them, but this has little significance since the organism had been in artificial culture for a considerable time and

[1] Barker and Grove's organism was found by Miss Doidge (2, p. 58) to give no growth in Uschinsky's solution. This was not my experience. Slight growth resulted and the liquid became strongly alkaline, then bleached at the bottom and a gelatinous precipitate was formed.

might well have lost its original parasitic properties. Careful observation will therefore be made next spring for signs of either disease, and it is hoped that the question of identity in etiology may then be definitely settled.

A disease of Mushrooms has previously been found by Tolaas (6) in which the symptoms were identical with those here described. His description of the causal organism is rather meagre, but in such reactions as are given, except in two instances, there is complete agreement with those of the organism described in this paper. The exceptions are in the reduction of nitrates and in the action upon starch (see comparative schedule, p. 218). It is not clear from his brief statement "Nitrates are reduced" how Tolaas arrived at this conclusion, and, in fact, it is possible that both in this and in testing the action of the organism upon starch the methods of technique employed by Tolaas were different from those employed by the authors, and have led them to opposite conclusions. Putting aside these two characters the organisms are closely similar, and, since the symptoms of the disease correspond exactly with those described by him, there seems little doubt that we have here the disease discovered by Tolaas. He suggests that the organism may be a parasitic strain of *Pseudomonas fluorescens*. This may indeed be the case, but until it is proved it seems well to give the mushroom disease organism a distinguishing name, and, in spite of the slight disagreement in physiological behaviour, the organism here described is believed to be identical with that of Tolaas and the name *Pseudomonas Tolaasi* is suggested. The organism, however, may yet be shown to be identical with that of Barker and Grove, in which case it will be necessary to re-name it in order to give due priority to these investigators.

Control Measures. Means of controlling the disease have not been investigated for the reason that it subsided and disappeared naturally. Tolaas found an efficient method of prevention of the disease in the fumigation of the beds with sulphur previous to spawning. In this connection it is of interest to note that sulphur fumigation has been the general practice in the houses at Brentford, but was abandoned for the season in which the outbreak occurred.

Comparative Schedule.

	Mushroom Disease.		Pear Blossom Blight.	
	Organism of Tolaas	Organism of Paine	Organism of Barker and Grove	Organism of Doidge
1. Dimensions	$1{\cdot}0\mu$–$1{\cdot}5\mu \times 0{\cdot}5\mu$	$0{\cdot}9\mu$–$1{\cdot}7\mu \times 0{\cdot}4\mu$–$0{\cdot}5\mu$	2μ–$4\mu \times 0{\cdot}5\mu$–$0{\cdot}8\mu$	$0{\cdot}5\mu$–$3\mu \times 0{\cdot}45\mu$–$0{\cdot}7\mu$
2. Flagella	Polar 1 to 2	Polar 1 to 2, occasionally 3, 4 or 5	Polar 3 to 6	Polar 1 to 5
3. Capsule	—	Absent	Absent	Present
4. Optimum temperature	—	25° C.	18° C.	25° C.
5. Thermal death point	—	49°–50° C.	47°–48° C.	49° C.
6. Colour	Fluorescent	Fluorescent	Fluorescent	Fluorescent
7. Bouillon	Well clouded in 36 hours; pellicle and ring—very thick in some cases	Well clouded in 24 hours; thick pellicle in early cultures; thin pellicle and ring in later cultures; very viscous—mucoid	Slightly clouded in 24 hours; slight rim and pellicle; gelatinous precipitate	Well clouded in 24 hours; tendency to pellicle formation; considerable viscid sediment
8. Gelatine stab	Liquefaction saccate	Liquefaction infundibuliform; granular precipitate; growth in upper part of stab only	Liquefaction crateriform; white precipitate; no liquefaction along stab	No liquefaction; growth in upper part of stab only
9. Agar colonies	Shining greyish-white; greenish pigmentation of the medium	Round, raised, wet-shining; later lobed and spreading; greenish precipitate in medium	Round, raised, wet-shining; later lobed and spreading	Spreading irregular margins
10. Uschinsky's solution	No acid; no gas	Alkaline; no gas; bleached; mucoid deposit	Alkaline; no gas; bleached; very little growth	Heavy viscid deposit
11. Litmus milk	Coagulated; alkaline whey; complete digestion of casein	Coagulated; alkaline whey; partial digestion of casein; fluorescence	No coagulation; alkaline; complete digestion of casein	No coagulation; colour unchanged at first, bleached later; slow digestion of casein
12. Indol formation	Slight	Slight	None	None
13. Nitrate reduction	Reduced	Not reduced	Not reduced	Not reduced
14. Diastatic action	None	Feeble	Feeble	Feeble
15. Group number	221·2333133	221·2332123	221·3332123	222·2332123

SUMMARY.

A disease of cultivated mushrooms is described in which patches of a chestnut brown colour so disfigure the pileus as to render the affected crop quite unmarketable.

The disease is identical with that described in America by Tolaas, but left unnamed by him.

The cause of the disease is a small bacterial parasite which may possibly be a strain of *Pseudomonas fluorescens* and may prove to be identical with the organism which produces Pear-blossom Blight.

Until its identity is established by further experiment it seems well to give it a distinguishing mark, and the name *Pseudomonas Tolaasi* is suggested.

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PHYSIOLOGICAL PRE-DETERMINATION: THE INFLUENCE OF THE PHYSIOLOGICAL CONDITION OF THE SEED UPON THE COURSE OF SUBSEQUENT GROWTH AND UPON THE YIELD.

IV. REVIEW OF LITERATURE. CHAPTER III.

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CHAPTER III

THE EFFECT OF CONDITIONS DURING GERMINATION AND IN THE EARLY SEEDLING STAGE UPON SUBSEQUENT GROWTH AND FINAL YIELD.

Introduction.

The external conditions operating upon the seed during the critical stages of germination play an important part in determining the vigour of growth and the yield of the resulting plant. A variety of methods have been employed in endeavours to stimulate and accelerate seed-germination, but in few cases have the effects upon subsequent growth and final yield been studied. The experiments in which this has been

done, although few in number, are of considerable interest because they point to methods by means of which an action induced during germination may favourably or otherwise affect the whole course of development.

In many cases treatments of the seed previous to or during germination have been devised primarily with a view to seed-sterilisation and fungus control or with a view to increasing the percentage of seeds able to germinate. It has thus happened that observations on the physiological behaviour of the plants produced from these treated seeds have in most cases been incidental. This is unfortunate because in many cases an increase in the vigour and size of the seedlings has been noted, and because there is considerable evidence to show that a very close correlation exists between the size and vigour of the seedling, even in its earliest stages, and the final yield of the adult plant.

For instance, in the last report of the Experimental and Research Station of the Nursery and Market Garden Industries Development Society, Cheshunt, it is recorded as a result of a series of careful quantitative experiments carried out by Mr F. G. Gregory (16) that in the case of cucumbers a correlation exists between the area of the cotyledons and the dry weight of the plant after 30 days[1], also between the growth rate of the main stem and laterals and the weight of fruit produced in the first two "flushes." It is obvious that such observations are of great importance to horticulturists since they enable the practical man to forecast the future efficiency of a plant from the seedling stage.

On the one hand recent work is tending to establish that the ordinary variations observed in the size and vigour of seedlings are reflected in the size of the final yield independently of the environmental conditions obtaining throughout the main period of the plant's life. On the other hand it is known that a large number of easily applicable, brief treatments of seeds previous to and during germination, favourably affect the size and vigour of the seedlings produced. But practically no attempt has hitherto been made to bring these two facts together and to discover whether increased size and vigour of seedlings due to seed-treatments will pre-determine an increase in the size of the final yield independently of the conditions obtaining during the main period of growth, in other words, whether increased yields can be obtained as the result of simple

[1] The authors are indebted to Mr Gregory for permission to make use of the following unpublished data:—

For correlation between	(i) Maximum area of the cotyledons (ii) Dry weight of the entire plant after 30 days	$r = +\cdot 36$.
For correlation between	(i) Maximum area of the cotyledons (ii) Maximum area of the first foliage leaf	$r = +\cdot 54$.

seed-treatments. When once the position is defined it becomes apparent that such tests might give positive results, and, if so, would be of considerable practical value owing to the simplicity, brevity, and cheapness of the operations involved.

In the following review we shall have to deal with a very wide range of seed-treatments. It therefore seems advisable to briefly consider, under the headings of the various arbitrary methods employed, the results which have been reported in the literature, and subsequently to deduce as far as possible our general conclusions from the whole of the available evidence.

Treatments of the Seed affecting the Nutrition of the Seedling.

We may classify the treatments affecting nutrition and deal with them under the following headings:

(*a*) Removal or Partial Removal of the Cotyledons, Endosperm, etc.

(*b*) Soaking Treatments;

(*c*) Seed Impregnation Treatments (*i.e.* treatments in which the seeds are soaked in solutions of nutrient salts);

(*d*) Enzyme Treatments.

(*a*) *Removal or Partial Removal of the Cotyledons, Endosperm, etc.*

An obvious method of varying the amount of reserve food-material available for the developing embryo has been to remove, or partially remove, the cotyledons of exalbuminous seeds or the endosperm of albuminous seeds. In this way series of plants with decreasing initial supplies of food-material available for the seedling have been compared with plants from untreated seeds. But it should be borne in mind that not only have the food-reserves been removed with the cotyledons, but also a certain proportion of the initial assimilating surface of the plant. This factor appears to have been entirely overlooked by the original workers.

Experiments conducted on these lines are worthy of considerable attention for although the treated seeds do not, of course, give results showing increased yields, yet they clearly demonstrate the potentiality for pre-determination which exists during the early stages in the development of the seedling. The effects of the amount of nutrient material originally available for the embryo are found in the case of annuals to last throughout the life of the plant, and to be clearly visible during the stages of vegetative development, of flowering, and of seeding.

Some of the earliest workers to record results of experiments dealing with the effects of removing part of the seed-reserves are Tautphoeus (35), Marek (28), and F. Haberlandt (18). These investigators worked with a considerable number of annuals, including plants with albuminous and exalbuminous seeds. They carefully cut off fractions of the endosperm or cotyledons and sowed the seeds on damp blotting paper, but the embryos were not provided with any artificial food-material. The seedlings thus produced were compared with normal seedlings grown under similar conditions[1]. The main facts which emerged from their results were, that the life-duration of the embryo plant in the absence of other food supplies was directly related to the amount of food-material supplied from the cotyledons or endosperm, and that the size of all the organs developed also bore a direct relation to the amount of food-material originally available.

The interesting implication of these early experiments, namely, that the effect of the food-reserves of the seed on the early growth of the embryo would continue throughout the life of the plant if the seedlings were afterwards artificially supplied with nutrient salts, was followed up by Wollny. In a series of experiments with peas grown in water-culture solutions Wollny (41) first showed that the amount of growth made by plants during the first month of development was directly proportional to the amount of food-material originally available for the embryo. The following table summarises the results of two of his experiments:

[1] The question has sometimes been raised as to whether embryos which have been completely deprived of their food-reserves immediately previous to germination are able to develop at all. There seems to be no doubt, however, that if the requisite food be artificially supplied in the form of simple substances, such as sugar and simple salts, development can take place.

Dubard and Urbain (9) reported that the endosperm was never indispensable to the development of the plant. They supplied embryos of wheat, oats, barley, *Ricinus*, etc. with Knop's solution during their early stages of growth, and subsequently planted them in ordinary soil and obtained mature plants. Brown and Morris (3) reared perfect plants from excised barley embryos fed during their early stages with cane-sugar and mineral nutrient-solutions, and kept in the light.

With regard to exalbuminous plants, on the other hand, such as the bean, cauliflower and savoy cabbage, Dubard and Urbain (10) found that they could not obtain development under the same conditions unless the cotyledons were left attached to the embryo for a period varying from 7 to 10 days, but Buckner and Kastle (4), who carried out experiments with Lima bean embryos deprived of their cotyledons, found that while development could not take place in the presence of salt solutions only, yet development became possible if reducing sugars were supplied to the embryos.

TABLE I (after Wollny).

Experiment I (1874).

Pea seedlings from entire seeds compared after 30 days with those from seeds from which one cotyledon had been removed. The seedlings were provided with nutrient solutions. Six seedlings in each experiment.

	Entire seeds (weight of a single seed = 0·405 gm.)	Treated seeds (weight = 0·202 gm.)
Average weight of the aerial parts of the plants	2·380 gm.	1·207 gm.
Average weight of the roots...	0·872 gm.	0·403 gm.
Average breadth of the main root	118 units*	108 units*
Average length of the plants	35·16 cm.	29·63 cm.
Average breadth of the internodes	185 units*	151 units*

Experiment II (1875).

Pea seedlings from entire seeds, seeds with ½, and seeds with ¾ of their cotyledons removed, compared after 4 weeks. The seedlings were provided with nutrient solutions. Four seedlings in each experiment.

	Entire seeds (weight of a single seed = 0·405 gm.)	Seeds with ½ cotyledons	Seeds with ¼ cotyledons
Average weight of the aerial parts of the plants... ...	3·423 gm.	2·016 gm.	1·209 gm.
Average weight of the roots...	1·205 gm.	0·679 gm.	0·635 gm.
Average length of the plants...	51·9 cm.	43·7 cm.	33·8 cm.
Average breadth of the internodes	168 units*	146 units*	127 units*

* 1 unit = 0·01428 mm.

Wollny subsequently conducted experiments with peas, vetches and winter rye in which the development of the plants, which were grown in soil under ordinary conditions, was followed through its *whole course*. The results obtained from entire seeds were compared with those obtained from seeds from which ⅓ and ⅔ of the cotyledons or endosperm had been removed. These results are given in Table II.

The total yield was very much larger in the case where entire seeds were used than in the case of seeds with ⅔ cotyledons or endosperm, and likewise very much larger again in the case of seeds with ⅔ cotyledons or endosperm than in the case of seeds with only ⅓ of their food-reserves available; but in contrast to the results obtained from the short-period experiments, the ratio of the final yields was not the same as the ratio of the amounts of initial food-reserves. The yield relative to the amount of reserve-material originally present was greater where the original food-reserve was small (see column X in Table II). Wollny (*l.c.*) summarises

his results in the following words: "Die Erträge in dem Grade steigen, als das Saatgut reicher an Reservestoffen ist, oder mit anderen Worten, die Verletzungen, welche die Reservebehälter der Samen treffen, in dem Grade ihres Umfanges das Produktionsvermögen der Pflanzen schädigen. Das relative Produktionsvermögen der Pflanzen im umgekehrten Verhältnisse zur Menge der Reservenährung des Saatgutes steht."

TABLE II.

The seeds were first allowed to swell in water and were then divided into three groups, viz. (i) seeds from which ⅓ of the cotyledons or endosperm was removed, (ii) seeds from which ⅔ of the cotyledons or endosperm was removed, and (iii) seeds which were not treated (=controls). The seeds were then sown in plots which were 4 sq. m. in area, a distance of 20 cm. being allowed between the seeds.

Name of plant	Condition of the seeds	Weight of 100 seeds sown	Number of plants	Yield, on basis of 100 plants*		Number of plants at the harvest	X Yield relative to the amount of reserve-material originally present
				Seeds	Straw		
		gm.		gm.	gm.		
Peas	Entire seeds	31·5	100	*583·5*	2012	84	19·5
	Seeds with ⅔ cotyledons	21·0	100	*499·0*	1482	83	24·8
	Seeds with ⅓ cotyledons	10·5	100	*310·5*	1169	63	30·6
Vetches	Entire seeds	34·2	100	*310·8*	1138	87	10·9
	Seeds with ⅔ cotyledons	22·8	100	*291·2*	922	77	13·8
	Seeds with ⅓ cotyledons	11·4	100	*196·6*	526	49	18·2
Winter rye	Entire seeds	3·6	100	*863·4*	1510	96	241
	Seeds with ⅔ endosperm	2·4	100	*677·6*	1148	81	283
	Seeds with ⅓ endosperm	1·2	100	*580·8*	909	22	485

* If the number of plants actually present at the harvest be taken into consideration, the differences in yield become much greater.

The results of these German agriculturists do not appear to have attracted much attention. Some thirty years later a number of French workers (Delassus, Dubard and Urbain, and Urbain) turned their attention to the same subject. These investigators were not working so directly from the economic point of view and their results, while confirming those of the earlier German workers, enter into greater details, and we may profitably describe the results obtained by them.

E. Delassus (7) experimented with beans, vetches, and lupins, new seeds of the same origin, and, as far as possible of the same weight, being selected. These seeds were soaked in water for 24 hours, after which treatment they were divided into four lots, viz.:

Lot I. Entire seeds (= controls);

Lot II. Seeds from which one half of one of the cotyledons was removed;

Lot III. Seeds from which one whole cotyledon was removed;

Lot IV. Seeds from which $1\frac{1}{2}$ cotyledons were removed.

The seeds were then planted in uniform soil and received similar cultural methods. Morphological differences manifested themselves throughout the course of development. The suppression of a part of the food-reserves of the seed resulted from the outset in a retardation in the growth of the stem which lasted throughout the life of the plant. This fact is brought out in the following table, where the mean height of the stems of the beans and vetches at the end of the first three months of their development is indicated.

TABLE III.

	Mean height of stem after					
	1 month's growth		2 months' growth		3 months' growth	
	Beans	Vetches	Beans	Vetches	Beans	Vetches
Lot I	82 mm.	103 mm.	204 mm.	225 mm.	362 mm.	770 mm.
Lot II	39	76	96	187	328	675
Lot III	30	73	78	177	260	670
Lot IV	36	63	60	154	200	590

The number and size of the leaves and also the total fresh and dry weights of the aerial parts of the plants at each stage in their development remained approximately proportional to the amount of reserve food-material originally at the disposal of the embryo, as the following figures show:

TABLE IV.

		1 month's growth				2 months' growth				3 months' growth			
		Lot I	Lot II	Lot III	Lot IV	Lot I	Lot II	Lot III	Lot IV	Lot I	Lot II	Lot III	Lot IV
Number of leaves produced after													
Beans		10	6	4	5	21	12	9	8	34	21	14	13
Vetches		29	23	24	17	165	117	126	77	327	240	228	176
Dimensions of the leaves													
		mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
Beans	Breadth ...	33	18	17	18	35	34	31	21	38	40	36	33
	Length ...	51	31	27	28	54	50	34	28	55	57	49	45
Vetches	Breadth ...	6	4	4	3	10	8	9	7	—	—	—	—
	Length ...	52	45	41	31	75	74	69	64	83	84	70	78
Weight of the aerial part of the plant in gms.													
Beans	Fresh weight	49·9	35·2	17·4	16·5	—	—	—	—	—	—	—	—
	Dry weight	5·3	2·6	1·7	2·2	—	—	—	—	—	—	—	—
Vetches	Fresh weight	18·5	9·9	11·3	4·9	185	102	138	51·5	890	417	406	260
	Dry weight	2·6	1·5	1·7	0·7	25·5	14	18	8	183	83	77·5	49·1

A study of the root system is also interesting. Removal of the food-reserves appears to bring about a progressive disappearance of the secondary roots. The main root in the case of plants belonging to Lot I, is not always clearly distinguished; on the other hand, in the case of the plants belonging to Lots II, III, and IV, it shows a vigorous development.

The time of flowering and the total number of flowers produced were also influenced by the amount of reserve food-material available for the embryo. Every plant flowered, but, in the case of the plants belonging to Lots II, III, and IV, the flowers were produced later than in the case of the controls; and whereas there were on an average 36 flowers per stalk in the case of the beans belonging to Lot I (*i.e.* the controls), there were only 20, 16, and 10 flowers per stalk respectively in the plants belonging to Lots II, III, and IV.

The fruits were heavier and more numerous on the control plants, the average weight of 100 bean seeds harvested the same day being as follows:

Lot I	*Lot II*	*Lot III*	*Lot IV*
245 gm.	170 gm.	137 gm.	119 gm.

In conclusion the author made a further interesting observation, namely, that the suppression of the seed-reserves markedly decreased the power of the resulting plant to resist the attack of parasitic fungi.

In a later investigation Delassus (8) examined in detail the morphological modifications brought about by the complete or partial removal of the cotyledons of a number of leguminous plants, including the bean (*Vicia Faba*) and lupin. He followed the same routine as in the previous experiment. It was found by microscopical examination that the various tissues of all the organs of the plants produced from the treated seeds were reduced in size in proportion to the amount of cotyledonary tissue removed, and that this reduction was not only in the number of the constituent cells but also in the dimensions of individual cells. This reduction in tissue development was observable at the outset and persisted throughout the life of the plant[1].

With regard to albuminous seed (into which class the cereals fall) the method usually adopted has been to completely remove the endosperm (or perisperm) before germination or at various intervals after the commencement of germination. The effects upon the subsequent

[1] The influence of food-reserves is most marked in the earliest hours of germination, but their removal at quite a late stage in the development of the seedling may still give results similar in nature to those reported above, as is shown by the results obtained by Gain (14), who removed the cotyledons from lupin seedlings on the 12th day after sowing.

development of the plant of the removal at an early stage of the endosperm of albuminous seeds are in the main quite similar to those that occur in the case of exalbuminous seeds deprived wholly, or in part, of their cotyledons.

J. A. Urbain (36) in 1913 carried out experiments with oats, maize, fennel, *Saponaria* sp., *Nigella hispanica*, *Papaver somniferum*, and *Ricinus communis*. As in the case of Delassus' experiments, this author found that the effects produced as the result of removal of the seed-reserves were not merely temporary, from which the plant might recover after it had become established, but persisted throughout the whole course of its development. In all the species tested the effects were the same in character; the suppression of the endosperm (or perisperm) led to a dwarf habit, obvious modifications in the external morphology of the leaves, precocious flowering, sometimes followed by a second flowering, and frequent sexual anomalies in the course of the first flowering period.

It is of interest to record in some detail a single experiment of Urbain's in illustration of his results. Embryos of *Ricinus communis* were isolated from their food-reserves on the second day of germination and were kept in a greenhouse at 25° C. until the 12th day, when they were "potted out." On the 35th day they were transplanted to open ground together with controls. On the 47th day the controls were 1 metre in height whereas the experimental plants were only $\frac{1}{5}$ metre in height. The controls had the usual 9-lobed leaves, but the leaves of the treated plants possessed only 4 lobes. Flower spikes had appeared in the axil of the 4th leaf only in the case of the treated plants, the male flowers on these flower-spikes exhibiting various abnormalities. During this flowering period the growth of the treated plants was arrested, but the plants subsequently continued their growth. About the 74th day the controls produced flowers, and at the same time the plants from the treated seeds produced a second crop of flowers, the controls being at this stage 2 metres high as against $\frac{1}{2}$ metre in the case of the experimental plants.

Results of a similar nature were obtained with the other albuminous seeds investigated by Urbain (*e.g.* oats, maize, fennel, etc.).

Consideration of the above experiments, both of the earlier German agriculturists and of the more recent French school, strongly suggests that the influence exercised upon the plant throughout its development by the food-reserves of the seed is a phenomenon which needs further examination.

The work of Gressler (17), Hackenberg (19), Kiltz (23), and Gericke (15) throws perhaps the best light upon this question. These authors obtained dry weight measurements from week to week. From the data so obtained a complete analysis of the normal growth as compared with the growth of plants from which various amounts of the initial food-reserves had been removed, can be made.

The following table and figures (Table V and Figs. 1–3) summarise some of the results obtained by Gericke (*l.c.*) with *Helianthus annuus*, var. *Bismarckianus*. The results obtained with (*a*) normal plants, (*b*) plants from which one cotyledon and one foliage leaf were removed at a very early stage, and (*c*) plants from which both cotyledons were removed, are represented.

TABLE V.

Increase in dry weight of A. *normal plants of* Helianthus annuus Bismarckianus; B. *plants from which one cotyledon and one foliage leaf had been removed; and* C. *plants from which both cotyledons had been removed.*

Growth period in weeks	Dry weight of five plants A	B	C	Ratio $\frac{B}{A}$	Ratio $\frac{C}{A}$
1	·0571	·0489*	·0343*	·856	·601
2	·159	·0742	·0671	·466	·422
3	·579	·145	·182	·255	·314
4	2·008	·525	·463	·261	·231
5	6·225	1·863	1·163	·299	·187
6	→ 16·871	6·325	2·594	·375	·154
7	38·23	17·81	4·877	·465	·127
8	70·73	42·11	7·657	·595	·108
9	108·68	69·27	11·635	·638	·107
10	157·00	114·48	—	·729	—
11	230·00	—	—	—	—
12	310·43	—	—	—	—
13	403·00	—	—	—	—
14	504·00	—	—	—	—
15	631·00	—	—	—	—
16	707·00	—	—	—	—
17	769·00	—	—	—	—

The arrow indicates the point at which flower-bud formation begins in the case of normal plants.

* These figures may be taken as values of the *original* amount of food-reserves. The initial dry weight of the embryo, apart from the reserves, is negligible, and the seeds are exalbuminous. The cotyledons and foliage leaves were removed from the experimental plants during the first week of growth after the embryo had absorbed part of the food-material stored in them.

With regard to the growth of the normal plant the general law was formulated to the effect that during the vegetative growth period *the dry weight of the plant increases according to the principle of a geometric series*[1]. This law amounts to a statement that the total dry weight of the plant increases on a "compound interest" basis. From this law it follows that there are two main factors which control the final yield:

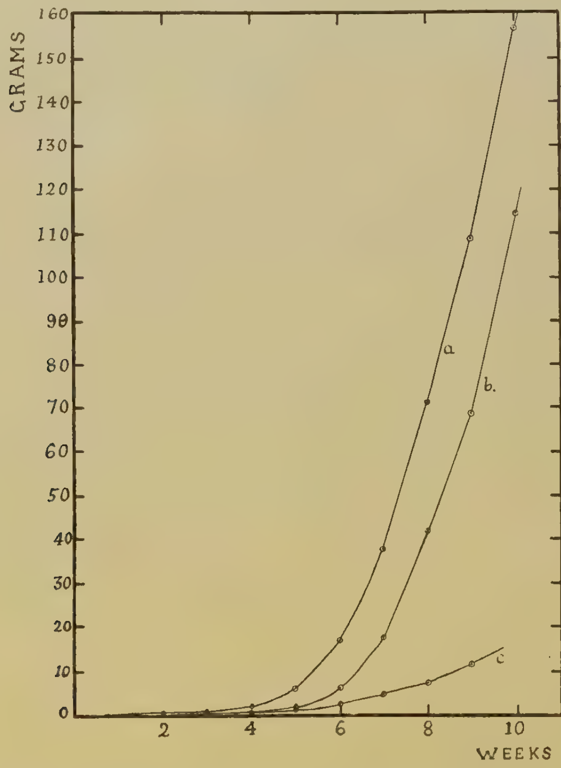

Fig. 1. Total dry-weight increase in the case of *a*, normal plants of *Helianthus annuus Bismarckianus*; *b*, plants from which one cotyledon and one foliage leaf had been removed; *c*, plants from which both cotyledons had been removed. (After Gericke.)

[1] The results of a series of investigations, which were carried out in Germany on the suggestion of the Ministry of Agriculture, and which were recorded in the *Landwirthschaftliche Jahrbücher*, 1877–79, supply a mass of detailed data with regard to the normal growth, the increase in dry-weight, and the change in leaf-area of a number of cultivated plants. These data appear to support the general law formulated above.

(1) the initial "capital," and (2) the "rate of interest[1]." The first of these factors has a pre-determining effect upon the development of the plant and cannot be influenced by subsequent environmental conditions, but the second factor would naturally be under the influence to some extent of the environmental conditions obtaining during the main growth period of the plant.

Curve *a* in Fig. 2 shows the change occurring from week to week in the "rate of interest" of the growth of normal plants. In this case the "rate of interest" or, in other words, the "efficiency" of the plant is at its maximum during the second week of growth and subsequently gradually falls throughout the course of later development[2].

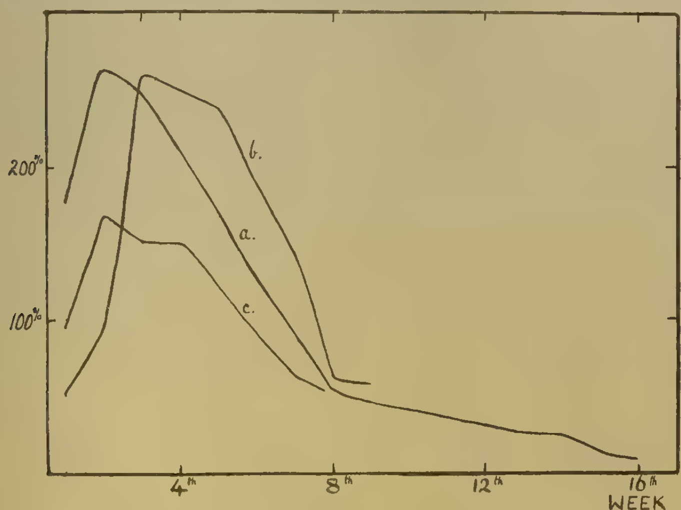

Fig. 2. Change in the percentage increase in dry weight from week to week (*i.e.* "rate of interest") in the case of *a*, normal plants of *Helianthus annuus Bismarckianus*; *b*, plants from which one cotyledon and one foliage leaf had been removed; *c*, plants from which both cotyledons had been removed.

[1] The German authors used the expression "Substanzquotient," which is the dry weight of the plant at time n divided by the dry weight of the plant at the time $n-1$. The unit of time taken is arbitrary and is one week. It seems to us more suitable to use the expression "rate of interest." The "rate of interest" = 100 (Substanzquotient − 1).

[2] In the case of the data obtained by Gericke the question which immediately presents itself is how far the fall in the "rate of interest" curve is due to inherent causes and how far it is due to the limiting factors of the environment, *e.g.* light. Gericke's data allow one to rule out temperature, but the author himself suggests the possibility of light as the limiting factor. The seeds were sown during the end of May and the beginning of June.

We may now consider for comparison with the normal plant the results obtained with plants from which different proportions of the initial food-reserves had been removed. Curves *b* and *c* (in Figs. 1 and 2) show that the removal of part of the initial food-reserves affects the subsequent growth and yield of the plant in two distinct ways. In the first place, broadly speaking the growth made by the plant, and consequently its final yield, is *approximately* proportional to the amount of food-material originally present; this may be called the pre-determining effect of the initial "capital." Secondly, the partial removal of the food-reserves has a specific pre-determining effect upon the "rate of interest," and it is in consequence of this fact that strict proportionality between the experimental and the control plants is not maintained.

The effect of loss of food-material upon the "rate of interest" is brought out in Fig. 2. In the case of the removal of one cotyledon and one foliage leaf the "rate of interest" is less than that of the control during the first three weeks. Later it increases rapidly, surpasses, and remains higher than that of the normal plant during the remainder of the growth period. Where both cotyledons are removed, however, the consequences are different. The "rate of interest" remains less than that of the normal plant throughout the whole course of development.

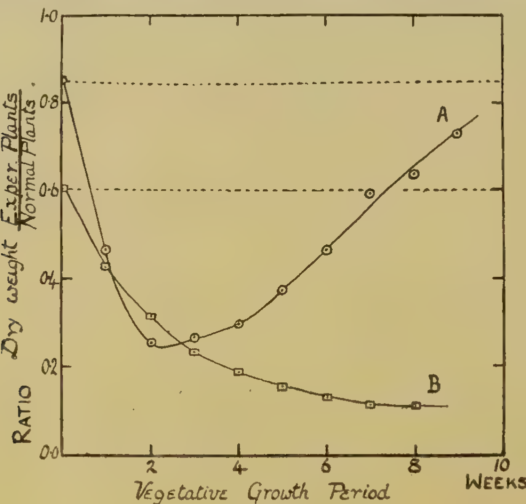

Fig. 3.

$$A = \frac{\text{Dry weight of the plants from which one cotyledon and one foliage leaf had been removed}}{\text{Dry weight of the normal plants.}}$$

$$B = \frac{\text{Dry weight of the plants from which both cotyledons had been removed}}{\text{Dry weight of the normal plants.}}$$

The manner in which this influence of the removal of part of the initial food-reserves upon the "rate of interest" affects the dry weight ratio is shown in Fig. 3, which is constructed from Gericke's data. Both sets of experimental plants are at the outset less productive relatively to the original dry weight than the controls. The ratio

$$\frac{\text{Dry weight of the experimental plants}}{\text{Dry weight of the control plants}}$$

decreases. In the later weeks of growth the development of the experimental plants from which one cotyledon and one foliage leaf had been removed differs widely from that of the plants from which both cotyledons had been removed. In the first case recovery sets in and the *relative* productivity rapidly increases and surpasses that of the controls so that at the end of the vegetative period the ratio $\frac{\text{Yield from the experimental plants}}{\text{Yield from the control plants}}$ is nearly the same as the ratio of the initial "capital."

In contrast, the plants from which both cotyledons had been removed, do not recover. They remain relatively less productive than the controls throughout their development and as a result, the final yields from the controls is nine times that from the experimental plants, whereas the initial "capital" of the controls was only $1\frac{1}{2}$ times that of the experimental plants.

Wollny, taking the weights of the final yields found, as we have stated above, that his plants, from which $\frac{1}{3}$ or $\frac{2}{3}$ of the cotyledons had been removed, were *relatively* more productive than those from untreated seeds, and it is seen that Gericke's data throw much light on Wollny's results.

We have still to seek an explanation for the following facts which were especially expressed by the French school of workers, namely—(1) that the seedlings which have been deprived of a large part of the food-materials elaborated by the parent-plant show symptoms characteristic of starvation although they may be equipped with all the organs necessary for the elaboration of their own food-supply (the removal of the parental supply would naturally be expected to cause only a slower and smaller initial growth); (2) that such seedlings commonly show in addition to starvation symptoms definite morphological abnormalities.

These two facts, taken together, seem to give some grounds for the view that the seedlings obtain from the food-reserves elaborated by the parent some nutritional elements necessary for normal growth and development which they cannot elaborate themselves except at some considerably later stage in their development.

In concluding this section dealing with the effect upon subsequent growth and final yield of the total or partial removal of the initial food-reserves of the plant, the main generalisation to be made on the basis of the evidence reviewed is that the yield from the plant is approximately proportional to the initial amount of food-reserves available for the embryo.

(*b*) *The effects of soaking seeds in water.*

The pre-determining effects of soaking seeds in water are often pronounced. From the point of view of growth and yield, it appears from the evidence we are about to review that these effects may be good or bad, the result depending upon the external conditions during the soaking treatment and upon its duration. How far this form of treatment is properly included here under the head of treatments affecting nutrition, is debatable. There is certainly a considerable exosmosis of soluble food-reserves from seeds soaked in water, and on the basis of such results as are described above, this should cause a depression in growth and yield. On the other hand, owing to the fact that actual growth is inhibited in the embryo under water, time is allowed for a complete mobilisation of food-reserves in readiness for very active growth as soon as the seed is sown, so that the early stages of development may be unusually vigorous. The advantage of considering in this place the question of the pre-determining effects of soaking seeds in water is that in dealing later with other seed treatments it will be found that soaking the seed in water is necessarily bound up with many of these[1].

In the late seventies and early eighties of last century a group of German workers, notably C. Kraus (25) and (26) and E. Wollny (42), investigated very fully the effect upon subsequent growth and yield of soaking seeds in water and obtained remarkable results. These authors emphasised the importance of the conditions under which the soaking was carried out, especially with regard to the relative amount of water employed. Beneficial effects upon growth and yield were obtained when the soaking of the seed was carried out with the least possible amount

[1] In the Wolfryn process of electrical treatment of seeds for the purpose of increasing the yield, cereal and other seeds are immersed in large tanks containing weak solutions of NaCl or other salts through which a direct current is passed. It is stated by the inventor, Mr H. E. Fry (see Letter to *Agricultural Gazette*, LXXXVIII, No. 2328, 1918, p. 138), that in the course of the experimental tests, it was found that although the electrically treated seeds gave the best results, the *soaking treatment alone* gave better results than no treatment at all.

of water, and they believed that the main effect of using as small an amount of water as possible lay in reducing the loss by exosmosis of essential soluble food-reserves during the process of soaking. It may be pointed out that the minimum amount of water is at the same time a favourable condition for the supply of oxygen to the seed and for the removal of carbon dioxide from the seed during soaking. The time of immersion employed varied from 24–100 hours according to the species of seed under investigation. Generally speaking the time of immersion allowed was just long enough for the swelling of the seed to become complete. These authors, in view of the possible economic application of this seed-treatment, carefully tested how far the re-drying of the seed would affect the results, and found that in general the re-drying of the seed after soaking, especially if carried out slowly, did not appreciably alter the beneficial influence of the process. The following general conclusions may be drawn from their experiments.

(I) *Effect on germination.*

(*a*) Seeds soaked in the minimum amount of water and afterwards *slowly dried* at ordinary temperatures imbibe water and develop more quickly, when again allowed to take up water and germinate[1], than untreated seeds.

(*b*) Seeds which are *rapidly dried* after the initial soaking germinate more slowly than untreated seeds.

(*c*) Seeds swollen in water and sown in the still moist condition germinate more quickly than untreated seeds.

(II) *Effect on subsequent growth and final yield*[2].

(*a*) In general, seeds soaked in water previous to germination give rise to slightly fewer plants than untreated seeds. If the seeds are re-dried too rapidly the number of plants produced may be considerably diminished.

(*b*) Soaking seeds in water previous to germination tends to accentuate individual differences in the growth of the plants produced from them.

(*c*) Plants from seeds swollen in water previous to sowing develop at first more quickly than those from untreated seeds, but this initial difference in growth tends to disappear later on.

[1] For detailed experiments dealing with this point see Tautphoeus (35).

[2] It is immaterial whether the seeds after swelling in water are *slowly* re-dried before sowing or whether they are sown at once in the moist condition.

(*d*) At a later stage the experimental plants take the lead, and flower before the control plants.

(*e*) The experimental plants have a longer growth-period and flowering-period than the control plants, arrive at maturity at a later date and give larger final yields, and this probably accounts for the fact that plants from seeds which are soaked in water previous to sowing are more productive than plants from untreated seeds.

(*f*) Soaking the seed in a relatively large volume of water, for instance, ten volumes of water to one volume of seed, reduces the beneficial effect, and may even be harmful.

(*g*) The soaking treatment is especially useful when the seeds are sown in light dry soil, provided that the seed is well covered with the soil.

In view of the importance of their results we may give in full an account of a few typical experiments carried out by Kraus (25) and by Wollny (42). Kraus carefully analysed at all stages of development of the plants the effect of the seed treatment. The following is a summary of the results of three of his experiments carried out with beans, peas, and seeds of *Lupinus angustifolium* respectively.

Experimental data.

Soil. Deep loamy sand (Keuper).

Previous History. Crop maize, stable manure applied.

Preparation of the Soil. In the spring the ground was dug deeply with a spade.

Cultivation of the Ground. Weeded and hoed.

Date of Sowing. April 26th.

Weather Conditions during Experiment:

	(*a*) Temperature			(*b*) Weather			
Month	Maximum	Minimum	Mean	Fine	Cloudy	Rainy	Changeable
April	7°	3°	5·4°	8	17	4	1
May	14	0	7·5	10	15	6	—
June	19	12	14·6	13	7	3	7
July	15	8	11·6	6	8	15	2
August	19	10	13·6	17	7	6	1

Kind of Seed used. Carefully selected large seeds.

Treatment of the Seed:

1. Untreated (=controls);
2. Swollen in water for 24 hours, afterwards *quickly* dried;
3. Swollen in water for 24 hours, sown in the moist condition.
   (During the soaking-treatment a few of the peas had sprouted.)

Spacing and Depth of Sowing:

	Spacing	Depth	Number of seeds in each row
Beans	15 cm.	4 cm.	42
Peas	10 cm.	3 cm.	42
Lupins	15 cm.	3 cm.	30

Harvested. August 30th.

The relative degree of development of the experimental and control plants at various stages was noted throughout the experiment. The results obtained were as follows:

XW = plants from seeds which were swollen and sown in the moist condition;
XD = „ „ „ and *quickly* dried;
C = controls (= plants from untreated seeds).

(i) *Beans.*

Comparative degrees of development at different periods	Order in which seeds sprouted	XW; C; XD
	1.	XW=C=XD
	2.	XW=C>XD
	3.	XW>C>XD
	4.	XW>XD>C
	Order in which plants ripened off	C; XW; XD.

(ii) *Peas.*

Comparative degrees of development at different periods	Order in which seeds sprouted	XW; C; XD
	1.	XW=C=XD
	2.	XW=C>XD
	3.	XW>C=XD
	4.	XW>XD>C
	Order in which plants ripened off	C; XW; XD.

(iii) *Lupins.*

Comparative degrees of development at different periods	Order in which seeds sprouted	XW; XD; C
	1.	XW=C=XD
	2.	XW>C=XD
	3.	XW>XD>C
	Order in which plants ripened off	C; XW; XD.

At the time of harvesting a very detailed analysis of every individual plant of the crop was made of which Table VI is a summary.

With reference to the yield it is to be noted in these experiments that the untreated seed is strictly comparable with the seeds sown in the swollen condition after soaking, but not with the seed sown after re-drying, because while in the former case the number of plants is the same per given area, in the latter case the plants are far fewer in number and consequently much wider spacing per p'ant is allowed..

Where a comparison therefore is legitimate, as between untreated seeds and seeds soaked but sown in the moist condition, the treatment clearly increased the yield in all three experiments; and this increase was correlated with modifications in development at all stages, as described above.

In the case of a comparison between untreated seed and seed quickly dried after soaking the yield *per plant* is markedly larger in the case of the treated seed, but the total yield per given area is smaller. Any conclusions drawn from the figures for the yield per plant are vitiated

TABLE VI.

Harvest results.

	Beans			Peas			Lupins		
	C	XD	XW	C	XD	XW	C	XD	XW
Number of seeds sown	42	42	42	42	42	42	30	30	30
Number of plants produced	42	9	42	39	17	40	26	15	27
							Main stem		
Average length of stem per plant	60 cm.	68·8 cm.	74·7 cm.	139 cm.	151 cm.	216 cm.	40·6 cm.	41·8 cm.	42·8 cm.
Average number of internodes per plant	18·6	24·7	21·8	—	—	—	—	—	—
Average number of pods per plant	6	13·8	8·2	6·4	8	7·6	43	68	53
Average number of pods per main stem	5·7	6·5	6·4	—	—	—	—	—	—
Average number of seeds per plant	15·8	43·8	20·7	22·2	28·7	35·7	—	—	—
Number of successive inflorescences	—	—	—	—	—	—	3·6	3·8	3·7
Percentage of plants that were branched	24	89	45	—	—	—	58	87	56
Percentage of pods fully ripe at harvest	—	—	—	40·6	25·5	9·7	—	—	—
Percentage of plants in which the pods were fully ripe at harvest	74	11	50	—	—	—	—	—	—
Total yield (*i.e.* total number of seeds produced)	*663*	*394*	*869*	*869*	*489*	*1429*	—	—	—
Percentage increase or decrease in total yield of experimental plants as compared with the controls	—	−41	+31	—	−44	+65	—	—	—

by the fact that the plants from the treated seed have a much wider spacing owing to the large mortality amongst them.

Wollny's (42) experiments extended over a number of years and his attention was directed more to the effect upon final yield of the soaking treatment of the seeds. The following tables give a detailed summary of his results.

The most noteworthy features of these results were firstly, that increased yields of grain were obtained in every case (with the exception of Winter Rye) as the result of the soaking treatment; and secondly, that a reverse effect, *i.e.* a decreased yield, was obtained when the swelling of the seeds was carried out in excess of water.

Since the publication of the work of Kraus and Wollny we have not been able to find in the literature any reference to the subject until

TABLE VII.

Comparison of Yields from (1) *seeds soaked in water and sown in the moist condition,* (2) *seeds soaked and redried before sowing, and* (3) *untreated seeds.*

The peas, beans, rye, and the vetch seeds were allowed to swell in the minimum amount of water for 36 hours, the maize for 72 hours. The re-drying process extended over 14 days during which the seeds were left exposed to the sun and air.

Kind of seed	Date of experiment	Treatment of the seed	Number of plants		Yield from 100 plants		Average weight of 100 seeds	Percentage increase or decrease in yield of seeds from experimental plants as compared with controls
			Original	At the harvest	Seeds	Straw		
					gm.	gm.	gm.	
Victoria peas	1877	Swollen, sown moist	64	58	_532·9_*	1324*	—	+29
		Untreated	64	59	413·3*	1443*	—	
Beans	1877	Swollen, sown moist	64	57	_920·5_*	2436*	—	+27
		Untreated	64	60	727·6*	2215*	—	
Victoria peas	1878	Swollen, sown moist	100	88	_1188·6_	1778	—	+23
		Untreated	100	94	967·0	1658	—	
Victoria peas	1882	Swollen, redried	92	74	_548·6_	1594	—	+ 9
		Untreated	97	76	502·6	1684	—	
Vetch	1882	Swollen, redried	90	79	_440·4_	910	—	+ 6
		Untreated	96	82	417·0	1074	—	
Winter rye	1882	Swollen, sown moist	100	96	867·0	1510	—	− 6
		Untreated	100	100	_925·0_	1690	—	
Victoria peas	1882	Swollen, sown moist	95	84	_602·0_	2012	—	+10
		Untreated	97	90	548·0	1998	—	
Vetch	1882	Swollen, sown moist	89	87	_414·0_	1138	—	+ 7
		Untreated	98	89	388·0	1146	—	
Victoria peas	1883	Swollen, sown moist	69	62	445·0	1355	—	+17
		Swollen, redried	79	71	_511·0_	1408	—	+34
		Untreated	93	83	382·0	952	—	
Beans	1883	Swollen, sown moist	99	99	_869·0_	1545	46·5	+ 9
		Swollen, redried	100	96	868·0	1459	45·6	+ 9
		Untreated	99	94	798·0	1468	38·8	
Winter rye	1883/4	Swollen, sown moist	99	60	1160·0	1983	2·99	− 8
		Swollen, redried	95	83	1101·0	1831	3·17	−13
		Untreated	93	70	_1263·0_	2314	3·14	
Summer rye	1884	Swollen, sown moist	94	80	497·0	975	2·75	+ 5
		Swollen, redried	85	53	_559·0_	1302	2·38	+18
		Untreated	89	78	475·0	1051	2·57	
Maize	1884	Swollen, sown moist	27	27	12515·0	46740	38·9	+11
		Swollen, redried	27	26	_14792·0_	47577	36·1	+31
		Untreated	27	27	11274·0	41630	36·4	
Victoria peas	1884	Swollen, sown moist	96	92	_730·0_	1282	27·9	+ 9
		Swollen, redried	92	87	705·0	1310	29·4	+ 5
		Untreated	94	87	668·0	1184	28·7	
Beans	1884	Swollen, sown moist	95	77	381·0	766	47·2	+ 3
		Swollen, redried	95	82	_402·0_	792	51·0	+ 9
		Untreated	94	80	369·0	725	47·7	

* Yield from 64 plants.

TABLE VIII.

The Harmful Effect of Soaking Seeds in Excess of Water.

In these experiments the volume of water used was ten times that of the seed.

Kind of seed	Treatment of the seed	Number of plants at the harvest	Yield from 100 plants: Seeds	Yield from 100 plants: Straw	Average weight of 100 seeds	Percentage decrease in yield of seeds from experimental plants as compared with controls
			gm.	gm.	gm.	
Summer rye	Untreated	78	*475*	1051	25·7	—
	Soaked	65	359	877	22·7	−25
Peas	Untreated	87	*668*	1184	28·7	—
	Soaked	84	546	1214	27·5	−18
Beans	Untreated	80	*369*	725	47·7	—
	Soaked	77	264	766	54·4	−28

1907, when two papers by Eberhart (11) and Schleh (33) respectively appeared. These authors took up the question as it was left by Wollny and Kraus.

Eberhart at the Agricultural Institute of the University of Jena tested the effect upon yield of soaking seeds of barley and beans. The result of a pot experiment carried out in triplicate with barley appeared to be the same in every way as that obtained by Kraus and Wollny, in other words, the soaking of the seed affected the whole course of development and increased the final yield (Table IX).

TABLE IX (after Eberhart).

Soil. Clayey loam rich in humus.
Kind of Seed. Barley (weight of 100 grains = 5·21 gm.).
Date of Sowing. April 21st.
Period of Soaking. 48 hours.
Temperature of the water. 10° Cel.
Height of Plants on May 16th. From untreated seeds = av. 13·1 cm. From seeds previously swelled = av. 15·9 cm.

Harvest results (August 5th).

	From untreated seed	From treated seed
Number of stems per pot	18·5	20·5
Average number of stems per plant	3·08	3·41
Average length of the stems	49·59 cm.	56·50 cm.
Average total weight of a plant	9·28 gm.	11·70 gm.
Average weight of heads per plant	4·52 gm.	5·73 gm.
Average weight of straw per plant	4·76 gm.	5·96 gm.
Average number of grains per plant	74·16	89·50
Average weight of the grains per plant ...	3·45 gm.	4·56 gm.

In the case of the pot experiments with beans, the effect of different soil-water-content (30 per cent. and 60 per cent.) upon the results obtained by the soaking treatment was ascertained. The effect of the soaking treatment upon yield was found to be independent of the amount of moisture in the soil. Similar results were obtained with oats.

Finally a field experiment with beans was described in which the yield from plants from untreated seeds was compared with that from plants from seeds swelled and afterwards redried. The results obtained are summarised below:

TABLE X.

Harvest Results.

	Number of plants*	Weight of pods	Weight of straw	Average length of the stem	Average number of pods per plant	Weight of seeds
Untreated seed	96	609·0 gm.	776·0 gm.	97·75 cm.	4·19	*474·3* gm.
Seed swollen in water previous to sowing	96·6	697·8 gm.	877·6 gm.	103·02 cm.	5·08	*543·3* gm. (+15 %)
Seed swollen in water and then redried previous to sowing	95·3	677·1 gm.	875·6 gm.	101·74 cm.	5·03	*526·3* gm. (+11 %)

* Mean of three experiments.

Schleh reported the following results of large-scale field tests with oats carried out to determine whether the soaking treatment of seeds was of any economic value. On moist soil with a high humus content[1]

[1] I. *Mechanical Analysis of the Soil.*

Size of sand particles	Surface soil of Plots 1 and 2	Surface soil of Plots 7 and 8
2–1 mm.	0·1 %	0·1 %
1–0·5 mm.	13·4	16·5
0·5–0·25 mm.	22·2	20·8
0·2 mm.	51·1	50·2
Silt	13·2	12·4

II. *Chemical Analysis of the Soil.*

	Surface soil of Plots 1 and 2	Surface soil of Plots 7 and 8
Organic matter	3·05 %	1·15 %
nitrogen	0·156	0·122
Mineral matter	96·95 %	98·85 %
sodium chloride ...	0·153	0·146
magnesia	0·109	0·090
potash	0·110	0·112
phosphoric acid ...	0·138	0·141

an increase of 90 kilograms of grain, 300 kilograms of straw, and 280 kilograms of chaff per hectare in favour of the treated seed was obtained. On dry soil with a low humus content, on the other hand, the plants from the treated seeds gave a slightly smaller yield than the controls to the following extent, 10 kilograms of grain, 4 kilograms of straw, and 20 kilograms of chaff per hectare. The seeds used in Schleh's experiment were soaked for 48 hours in distilled water.

The importance of the conditions under which the soaking treatment is carried out.

Although the soaking treatment appears to be simple, the immediate and subsequent effects of soaking seeds in water are complex, and differ widely according to the conditions under which the soaking of the seed is carried out.

During the natural uptake of water preceding germination the whole physiological system of the seed is set in motion. Enzymes are liberated, no doubt, from pro-enzymes, and soluble food-materials increase, etc.

When seeds are immersed in water for the purpose of swelling, the conditions to which the plant is subjected are abnormal, as is shown by the fact that germination is inhibited. Under these abnormal conditions there is no doubt that many of the complex of processes usually accompanying the initiation of germination are modified. In addition, however, it is definitely known that a considerable exosmosis of essential soluble food-reserves occurs[1], the supply of oxygen to the seed is decreased, and carbon dioxide accumulates in the seed.

It is obvious that both the leaching out of essential food-reserves, and the conditions of oxygen supply and of carbon dioxide escape, must be greatly influenced by such factors as time of soaking, temperature of soaking, relative amount of water used, movement of the water, surface of the water exposed to the air, size of the seed, and density of the seed-mass.

How far the leaching out of food-material and the modification of the rate of gaseous exchange under the abnormal conditions of soaking are related to the beneficial alterations in subsequent development and in yield observed has not been satisfactorily investigated. Wollny and his contemporaries considered that the leaching out of essential food-reserves was always detrimental and comparable to the partial removal of the cotyledons or endosperm as described above, and endeavoured

[1] See especially A. Zöbl (44), F. Haberlandt (18), T. Yokoi (43) and G. André (1). Data published by Zöbl and André show that the phosphorus and potassium of the seed-contents are very rapidly lost when seeds are soaked in pure water.

to eliminate such exosmosis as far as possible by using the minimum amount of water necessary for the complete swelling of the seed.

That the exosmosis of soluble food-material, or the lack of oxygen combined with accumulation of carbon dioxide which must necessarily accompany the immersion of the seed in water, may become sufficiently pronounced to cause very definite injury, resulting in a fall in germination percentage and a decrease in the subsequent yield, is clear from the work of numerous authors, and it is in this connection in particular that the conditions under which the soaking treatment is carried out are important. For example, if the seeds are immersed in a dense mass, even with a minimum amount of water, the lack of oxygen and accumulation of carbon dioxide resulting at normal temperatures from such conditions may in a very short time cause serious injury to the seeds, as the present authors have found. Again, it has been shown that in the case of some seeds (*e.g.* peas and beans) pronounced injury results even after very short periods of soaking when excess of water is used, probably for the same reason (cf. Kidd and West (21)).

If the temperature is high (*e.g.* 25°—30° C.) the injurious effects are more difficult to avoid; on the other hand, for some as yet unexplained reason, low temperatures (0°–10° C.) appear in many cases to exert a specific injurious action upon seeds soaking in water (cf. Kidd and West (22)).

In any case too long a period of soaking produces injury and death. Coupin (5) has shown that whereas some seeds can withstand only a brief period of immersion in water, others can withstand a long one.

The results of experiments in which stagnant water is compared with running water in its effect upon submerged seeds, indicate that lack of oxygen and accumulation of carbon dioxide, rather than the loss of soluble substances, are chiefly responsible for the injurious effects observed. In running water as compared with stagnant water, although a greater exosmosis of soluble matter occurs, the oxygen supply to the seed is maintained and carbon dioxide accumulation is reduced to a minimum. Under these conditions certain seeds can germinate and form roots and leaves (cf. Jodin (20)). In stagnant water, on the other hand, even when leaching is reduced to a minimum, germination is inhibited and injury and death eventually follow.

(*c*) "*Seed Impregnation*" (i.e. *Soaking Seeds in Solutions of Nutrient Salts*).

Wollny (41) and Tautphoeus (35) in the first instance, and later Schleh (33), Köch (24) and others, investigated the effect of soaking seeds in solutions of various nutrient salts upon their germination and subsequent growth and yield.

Table XI gives the results of experiments recorded by Wollny.

From the table (p. 245) it appears that the results obtained by the use of solutions of nutrient salts are not appreciably better than those obtained with pure water, and this general conclusion is supported by the results obtained by the other authors mentioned above. Schleh used (1) a 20 per cent. solution of potassium nitrate, and (2) a nutrient solution consisting of 5 per cent. phosphoric acid, 10 per cent. nitrogen, and 10 per cent. potassium, and soaked his seed for 48 hours.

(*d*) *Enzymes.*

The enzymes of the seed are primarily concerned in the physiological processes whereby the food-reserves are prepared for consumption and utilised in growth. Factors influencing in any way the utilisation of the food-reserves of the seed may have an important pre-determining influence upon the whole course of subsequent development of the plant.

In this connection two different lines of experiment have occurred to a number of investigators, namely:—

(i) To supply the seed artificially with those products which are likely to result from the breaking down of its own food-reserves under the action of enzymes (Sharpe (34)).

(ii) To supply the seed with the enzymes themselves (Babcock (2), Waugh (37) and (38), Lehmann (27)). Under this category may be included those treatments which are believed to stimulate enzyme action in the seed (Effront (13)).

It is unfortunate that the results recorded stop short either at germination or at the early seedling stage.

Babcock (*l.c.*) reports the results of an experiment conducted at the Wisconsin Agricultural Experiment Station with corn (*Zea Maïs*), less than 50 per cent. of which germinated after soaking in pure water. But seeds from the same lot and treated in the same manner as the controls, except that the water in which they were soaked contained commercial

Table XI.

Comparison of yields from seeds soaked in solutions of various nutrient salts with those obtained from (1) untreated seed and (2) seeds soaked in distilled water.

The peas were soaked for 24 hours, the beans for 36 hours.

The seeds were sown at a uniform depth of 5 cm.

Name of plant	Date of experiment	Treatment of the seed	Distance apart of the plants	Number of plants: Original	Number of plants: At the harvest	Yield from 64 plants: Seeds (gm.)	Yield from 64 plants: Straw (gm.)	Percentage increase or decrease in yield of seed from experimental plants as compared with the controls
Horse beans	1876	Soaked in distilled water	25 cm.	64	*64*	331	642	+11
		,, ·5 % solution of NaCl		64	55	*389*	740	+31
		,, ·5 % Knop's solution		64	63	305	587	+ 3
		Untreated (sown dry)		64	63	297	521	
Victoria peas	1877	Soaked in distilled water	25 cm.	64	58	533	1324	+29
		,, ·5 % solution of NaCl		64	57	*693*	1639	+68
		Untreated		64	*59*	413	1443	
Horse beans	1877	Soaked in distilled water	25 cm.	64	*60*	920	2436	+27
		,, ·5 % solution of NaCl		64	57	*951*	2755	+31
		Untreated		64	59	727	2215	
Victoria peas	1878	Soaked in distilled water	20 cm.	100	88	*1188**	1778*	+23
		,, ·5 % solution of NaCl		100	91	845*	2145*	−13
		,, ·5 % soln. of potassium phosphate		100	*97*	867*	1918*	−10
		,, ·5 % ,, ammonium nitrate		100	71	955*	2049*	− 1
		,, concentrated "Gyps." solution		100	89	1038*	1983*	+ 7
		Untreated		100	94	967*	1658*	

* Yield from 100 plants.

diastase, all germinated. The author remarks that "the increased vitality of the diastase lot was very noticeable." 100 per cent. germination was also obtained when seeds from the same lot were soaked for 15 hours in a 3 per cent. solution of glucose instead of water, thus indicating that lack of suitable food-material was the chief reason for the poor germination capacity of the untreated seeds.

Remarkable increases in germination percentages were recorded by Waugh (37) for old tomato seeds soaked previous to sowing in a 5 per cent. diastase solution as compared with similar seeds soaked in distilled water (Table XII). Waugh also remarked that the vigour of the young plants was often enhanced by the enzyme-treatment of the seeds.

TABLE XII (after Waugh).

	Kind of seed	Age, years	Time of soaking, hours	Percentage of germination: Soaked in water	Percentage of germination: Soaked in 5 % solution of diastase
Tomato	Hundred Day	12	168	12 %	84 %
	Hundred Day	12	48	34	70
	Early King Humbert	12	24	14	24
	Essex Hybrid	9	24	0	10
	Long Keeper	5	25	36	46
Cucumber: White Spine		5	48	44	54
Radish: Carmine Erfert		6	48	46	60

Although such results as these of Babcock and of Waugh and the similar results reported by others, for example, Lehmann (27), who treated seeds of *Epilobium hirsutum* with solutions of papayotin, trypsin, etc. and obtained increased percentages and vigour of germination, appear to be quite definite, we cannot readily accept the conclusion that they are to be explained as being due to the specific action of the enzymes added, for it is difficult to understand how such enzymes, when applied externally, can enter the seed. In contradiction to the above results White (39) states that the addition of dissolved ferments does not increase the percentage of germination of old seeds, and when any effect at all is produced, it is a tendency to lower it.

Experiments in which diffusible organic food-substances have been supplied to germinating seeds with a consequent increase in the germination percentage are more easily explained. Sharpe (34) obtained increased vigour and percentage of germination by germinating seeds in the presence of leucine or asparagin, substances which are of common occurrence in germinating seeds.

That food-substances can be utilised by the young embryo when it

comes into contact with them is clearly shown by the work of Brown and Morris (3), Buckner and Kastle (4), and others.

Brown and Morris in dealing with the utilisation of sugar by barley embryos, demonstrated the interesting fact that if cane-sugar be supplied to the seed in such a way that it can enter and come into contact with the embryo, it is utilised in growth in preference to the food-reserves in the endosperm, which are left untouched[1]. Barley grains, after 24 hours soaking, had their distal ends cut across and were then set with their proximal ends uppermost in loosely packed glass wool saturated with (*a*) distilled water, (*b*) a 3·5 per cent. solution of cane-sugar. Vigorous and normal growth followed in both cases, but when the grains were critically examined at the end of 4 days it was found that whereas in the case of (*a*) the endosperm was completely disintegrated and the starch had been attacked, in the case of (*b*) the endosperm was still as tough as before germination and the starch had scarcely been attacked.

Little definite evidence is available as to how far treatments, which stimulate germination, do so in virtue of their influence upon the rate of consumption of food-reserves by the embryo. It is probable, of course, that most of the many arbitrary treatments, which have been found to favour germination, bring about at the same time a quicker consumption of the food-reserves under the action of the specific enzymes concerned, but evidence is lacking in most cases as to the manner in which this result is produced.

In the case of acid treatments, which have been shown to increase the vigour of germination and of subsequent growth (see following chapter in this series), the enhanced rate of food-reserve consumption recorded as the result of these treatments may probably be attributed to the action of acids in liberating enzymes from pro-enzymes. Brown and Morris (*l.c.*) found that they could obtain a larger secretion of diastase from excised barley embryos when these were placed on a slightly acid medium than when laid on a neutral substrate. On a neutral gelatin medium they obtained from 50 barley embryos after 3 days an amount of diastase equivalent to 0·1186 gm. CuO (0·0708 gm. equivalent from the embryos and 0·0478 gm. from the medium). The corresponding figures when 0·0065 per cent. formic acid was added to the medium show a total diastase equivalent of 0·1450 gm. CuO, of which 0·0904 gm. was obtained from the embryos and 0·0546 gm. from the medium. This amounts to an increase of 22 per cent.

[1] Brown and Morris (*l.c.*) showed that the presence of assimilable sugars inhibited the secretion of diastase by the scutellum.

Reynolds-Green and Jackson (31 & 32) have also shown that acidity leads to the liberation of enzymes, and we may recall here Plate's (30) observation that the food-reserves of seeds treated with concentrated sulphuric acid for a few hours were completely utilised in 10 days, as compared with 15 days in the case of untreated seeds, and that the subsequent development of the plants from the treated seeds was correspondingly more advanced.

The work of Eckerson (12) and Effront (13) is also important in this connection. Eckerson set out to determine the limiting factor in the delayed germination of embryos of *Crataegus mollis*, which had previously been shown by Davis and Rose (6) to have a definite after-ripening period independently of the presence of their carpels and testas. Eckerson's results were not conclusive, but she demonstrated a slow increase in the acidity of the hypocotyledonary region of the embryo during the after-ripening period culminating in a sudden increase towards the end of this period. This sudden increase in acidity was correlated with the formation of enzymes and with germination. She also found that treating the embryos with hydrochloric, butyric, or acetic acid shortened the after-ripening period and hastened the appearance of enzymes.

Effront (*l.c.*) working with barley, found that treatment with lactic acid (2 gm. per litre) favoured germination and at the same time increased the amount of diastase present in the grains.

Conclusion.

The main conclusion which appears to emerge from this brief review is that the conditions operating during germination and the early seedling stage of the life-cycle of the plant are of the utmost importance, especially in the case of annuals and biennials, *i.e.* in the case of the majority of economic crops. Conditions operating during germination exercise a pre-determining influence upon subsequent growth and directly affect the yield. In many cases the value of the effects obtained are from the economic point of view out of all proportion to the cost of the treatments used.

The selection of vigorous seedlings is a common practice among horticulturists. It is recognised that some sort of correlation exists between the vigour of the seedling and that of the adult plant, and some recent scientific work (Gregory, *l.c.*) has quantitatively established this fact. But the proper deductions have not been made. The vigour of the seedling may be due either to hereditary causes or to environmental

factors which have operated previously to, or during, germination. It is obvious that the environmental conditions which obtain during germination affect the vigour of the seedling, and in the present review of literature attention has been directed to special seed-treatments which have been found to stimulate not only germination but also the growth of the plants produced. The critical question is therefore—Can we propound a law to the effect that increased vigour of seedling development due to environmental conditions as distinct from hereditary causes, is correlated with increased vigour of growth throughout the life of the plant and with increased yield independently of the subsequent environmental conditions?

Experimental work should be concentrated on this distinction. If the principle of physiological, as distinct from hereditary, pre-determination was fully established, many of the methods of seed-treatment which have been found to stimulate germination and the growth of the seedling could probably be developed, and employed in the field and greenhouse as a means of increasing production.

(*To be continued.*)

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ON FORMS OF THE HOP (*HUMULUS LUPULUS* L.) RESISTANT TO MILDEW (*SPHAEROTHECA HUMULI* (DC.) BURR.); III.

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In previous articles (1) (2) I have pointed out that certain seedlings of the wild hop obtained from Italy show immunity, or resistance, to the attacks of the mildew *Sphaerotheca Humuli* (DC.) Burr.

Under conditions in which other seedlings of the same parentage and age (to the number of several hundreds) became severely infected with mildew, certain individual seedlings remained persistently immune throughout the growing season for the two consecutive years 1916 and 1917. The present paper deals with the behaviour of these and several other seedlings during 1918 and previous years. The manner in which these plants when grown in the greenhouse were artificially inoculated and otherwise exposed to infection has already been described in detail ((1), p. 456).

The facts observed as to the degree of immunity shown by the various seedlings can best be described if we take the plants in groups and record their behaviour each season for the years during which they have been under observation. In the annual record of each seedling the following abbreviations are used:

G = grown in greenhouse, I = immune,
H = „ hop garden, S = susceptible.

The figures 1 to 3 indicate the amount of mildew present, 1 = mere trace of mildew; 2 = fair amount of mildew; 3 = plant very mildewed. The plants are all seedlings of the wild hop, raised at Wye from seed obtained from Vittorio, Italy.

Group 1. 4 seedlings (1–4) sex unknown.

Plants 1, 2, 3, 4[1]. { 1916 G (I),
1917 G (I),
1918 G (I).

These four seedlings, 1-year-old in 1915, have proved persistently immune as 2-, 3-, and 4-year-old plants (non-flowering) in the green-

[1] These are four of the seven seedlings noted in (1), p. 456 and (2), p. 88.

house, under the severest tests as regards constant inoculations, for three years. They have now been planted out (during the winter of 1918–19) in the Experimental Hop-garden (under Reference Nos. 316, OB 26, OE 14, DD 31) with the object of seeing what effect, if any, the different conditions of growth have on their resistance to mildew.

Group 2. 5 seedlings (5–9).

Plant 5. Ref. No. Z 42 ♂
1917 H (I),
1918 H (I); 3 "cuts" 1917/18 G (I).

Plant 6. Ref. No. Z 2 ♂
1917 H (I),
1918 H (I); 3 "cuts" 1917/18 G (I).

Plant 7. Ref. No. OD 19 ♀
1917 H (I),
1918 H (I); 3 "cuts" 1917/18 G (I).

Plant 8. Ref. No. Z 25 ♀
1916 H (I),
1917 H (I),
1918 H (I); 4 "cuts" 1917/18 G (I).

Plant 9. Ref. No. OA 49 ♀
1917 H (I),
1918 H (I); 2 "cuts" 1917/18 G (I).

These five seedlings have all remained immune in the hop-garden, and the "cuts" taken from them in the winter of 1917–18 proved immune in the greenhouse during the growing season of 1918.

The plant Z 25 first attracted attention in the hop-garden in 1916, since no mildew was present on it while the two seedlings (Z 24 ♀ and Z 26 ♀) on either side of it in the same row, and of the same parentage and age, were severely attacked both on the leaves and "hops." The same thing occurred in 1917; Z 24 and Z 26 were excessively mildewed, and it so happened that some lateral branches of Z 24 had grown out, reached the main stem of Z 25 and had climbed up it and produced very mildewed "hops" (strobiles) on branches closely interwound round those of Z 25 which bore perfectly healthy (immune) hops. In the case of the seedling OD 19, a strong lateral shoot grew out and twined round the main stem of OD 18 (a susceptible seedling of the same age and parentage) and produced healthy hops on branches intertwined with those bearing the excessively mildewed hops of OD 18.

It may be pointed out that with respect to all these seedlings (Z 2, Z 25, Z 42, OA 49, OD19), the incidence of the disease in the hop-garden in both 1917 and 1918 was such as to ensure their natural

inoculation from adjacent mildewed seedlings, most of which were affected to the severest extent. In every case, each of these five seedlings had mildewed plants on either side of it.

The following inoculation experiment was carried out on the seedling Z 25 in 1918. On June 10th several lateral shoots, 9 in. to 1 ft. long, produced from the main stem at about 5 ft. from the ground, were inoculated by "atomising" three leaves on each shoot with water containing conidia of *S. Humuli.* The seedlings Z 24 and Z 26 were of the same age and parentage as Z 25, and had proved in 1917 to be very susceptible (S^3). On June 30th the following results were noted:

Ref. no.	No. of shoots (3 leaves inoculated on each shoot)	No. of leaves infected on each shoot	Total no. of leaves infected
Z 24	6	2, 3, 3, 2, 3, 1	14
Z 25	6	0, 0, 0, 0, 0, 0	0
Z 26	4	3, 0, 3, 3	9

At this date the patches of mildew were small, but many were densely powdery with conidia. The infected leaves were picked off to prevent the spread of the mildew to the commercial part of the hop-garden.

The evidence would seem to show that these five seedlings of Group 2 (which are all 5-year-old flowering plants) remain immune to mildew, after being grown for four years in a hop-garden under ordinary conditions of cultivation and manuring; although under the same conditions a large number of seedlings of the same age and parentage have proved each season to be exceedingly susceptible.

Group 3. 9 seedlings (10 to 18).

Plant 10. Ref. No. OR 38 ♀

1914 G (I),
1916 H (S^1),
1917 H (S^2); 5 "cuts" 1916/17 G (I*),
H (S^3);

1918 3 cuts 1916/17, now in H; Ref. No. W 56 (S^2),
„ Y 28 (S^3),
„ Z 4 (S^3).
2 cuts 1916/17 G (I)
9 cuts 1917/18 G (I),

* See footnote 1, next page.

As a 2-year-old seedling OR 38 was persistently immune in the greenhouse ((1), p. 456), in 1914; that winter it was planted out in the hop-garden. It flowered there in 1916, and in October of that year it proved

to be susceptible to a slight extent, several of the leaves and one hop (strobile) being slightly affected. In 1917, in October, there was a fair amount of mildew (with perithecia) on the hops; and in 1918 by Sept. 7th there was a fair amount of mildew on the young leaves and by October the hops had become excessively mouldy, a considerable percentage of them being deformed or totally undeveloped owing to the attacks of the mildew.

During the winter of 1916–17, five "cuts" were taken from OR 38 and grown (in pots) during the season of 1917 in the greenhouse; these "cuts" proved to be immune, except that two of them showed a temporary and strictly local susceptibility[1]. Two of these five "cuts" taken in 1916–17 were kept in the greenhouse during 1918, and proved persistently immune. The remaining three "cuts" had been planted out, in the autumn of 1917, in the hop-garden, and, as young, non-flowering plants, all proved in October, 1918, to be susceptible. One plant (Ref. No. W 56), $1\frac{1}{4}$ ft. high, showed a fair amount of mildew on the leaves; one plant (Y 28), 5 ft. high, was very mouldy on the leaves and stems; the third plant[2] (Z 4), 5 ft. high, was very mouldy on the leaves.

During the winter of 1917–18 nine "cuts" had been taken from OR 38 and these were grown in pots in the greenhouse during 1918. These plants proved persistently immune, notwithstanding the fact that the parent plant was decidedly susceptible in the hop-garden both in 1917 and 1918.

Plant 11. Ref. No. OR 39 ♂
1914 G (I),
1916 H (S[1]),
1917 H (S[1]); 2 "cuts" 1916/17 G (I),
1918 H (? I); 2 "cuts" 1916/17 G (I); 6 "cuts" 1917/18 G (I).

This seedling, after proving immune as a 2-year-old seedling in the greenhouse in 1914, showed slight susceptibility in the hop-garden in October, 1916, one leaf each on two lateral shoots showing small patches of mildew. In 1917, in October, there was one small patch of mildew on the under-surface of one leaf of a lately-developed lateral shoot. In 1918 there was no mildew on the plant; as, however, no actual inoculations were made the immunity cannot be held to be definitely proved. During 1916–17 two "cuts" were taken from OR 39; these proved immune in the greenhouse for two consecutive seasons. Six "cuts" taken in 1917–18 proved immune in the greenhouse during 1918.

[1] The facts have been given in detail, and discussed, in (2), p. 84; 86.

[2] This was the "cut" which in 1917 has proved immune, in the greenhouse, in the Exper. 4 recorded in (2), p. 85.

Plants 12, 13, 14. Ref. Nos. V 91, V 92, V 93. Sex unknown.

Plants 12, 13, 14 {1916 G (I),
1917 G (I).

1918. All 3 plants now in H: Ref. No. V 91 (S¹),
„ V 92 (S¹),
„ V 93 (S¹).

These three seedlings as 2-year-old plants proved persistently immune in the greenhouse during 1916, and again during 1917[1]. In the autumn of 1917 they were planted out in the hop-garden, the plants grew during 1918 to the height of 5 ft. and all showed slight susceptibility—a very few patches of mildew being present on a few leaves both of V 91 and V 92, and one patch only on the under-surface of one leaf of V 93.

Plant 15. Ref. No. Z 14 ♂
1917 H (I),
1918 H (S^1); 3 "cuts" 1917/18 G (I).

Plant 16. Ref. No. Z 22 ♀
1917 H (I),
1918 H (S^2); 2 "cuts" 1917/18 G (I).

Plant 17. Ref. No. OB 34 ♀
1917 H (I),
1918 H (S^1); 3 "cuts" 1917/18 G (I).

Plant 18. Ref. No. HH 44 ♀
1917 H (S^1),
1918 H (S^1); 3 "cuts" 1917/18 G (I).

The above four seedlings all agree in their "cuts" being immune when grown in the greenhouse, although all the parents show some degree of susceptibility when grown in the hop-garden. Z 14 showed the merest trace of mildew on its leaves; Z 22 a fair amount of mildew on its "hops" and very occasionally a trace of mildew on its leaves; OB 34 was immune in 1918 except for one quite young "hop" (strobile) which alone was smothered in mildew in the conidial stage, and arrested in development, among some hundreds of healthy "hops"[2]; HH 44 showed in both years only a trace of mildew in its "hops."

The evidence given by seedlings in Group 3 shows clearly that one and the same plant[3] may be persistently immune when grown in the greenhouse and susceptible even to the highest degree when grown in the hop-garden.

Group 4. 4 seedlings.

Instances of "semi-immunity" have been noticed in the case of four seedlings. With regard to the seedlings Z 15 (♂) and OC 6 (♂), one

¹ These are three of the seven seedlings noted in (1), p. 456, and (2), p. 88.

² This case may possibly be compared with the strictly local susceptibility shown by one leaf of the "immune" plant of OR 38 in the greenhouse in 1917 (see (2), p. 86).

³ Adopting Dr J. Schmidt's terminology (see *Comptes Rendus Trav. Labor. Carlsberg*, XI, 153 (1915)) each "cut" taken from the parent plant is a "clone-plant,"—the "hop-clone" being all those plants derived from the same seedling by vegetative propagation.

"cut" of each was taken in the winter of 1917–18, and grown in the greenhouse during 1918. These two plants never became really infected throughout the season. On inoculation infection stopped short, after the formation of small blisters or "humps" on the leaves (which I have already described (3) as being frequently the first sign of infection); on the surface of these "humps" a meagre, scarcely white growth of mycelium with conidiophores took place which soon died away, leaving minute, brown patches of dead, epidermal cells at the place where the mycelium had been. In the hop-garden, Z 15 was recorded as having mildew to the second degree in 1917 and 1918; while OC 6 was recorded as having no mildew in either year.

The seedling Z 23 (♂), of which three "cuts" were tested in the greenhouse during 1918, was also "semi-immune" in a very similar manner. Inoculation of the leaves was followed by the formation of yellowish, translucent "humps" on the leaf, on which a very weak growth of mycelium took place, the mildew scarcely ever presenting a white patch and the conidiophores soon dying away. In the hop-garden Z 23 was recorded as (S^2) in 1917 and (I) in 1918.

The seedling OA 33 (♂), of which two "cuts" were tested in the greenhouse in 1918, was a little more susceptible, the patches of mildew produced after inoculation being larger and white and "powdery" with conidia; unlike the growth of mildew found on really susceptible plants, however, these patches did not remain white and enlarge, but died away, leaving behind yellowish, more or less translucent spots where the mycelium had been. In the hop-garden OA 33 was recorded as having no mildew on it during 1917 and 1918.

In all the cases recorded above, the immunity to mildew shown in the greenhouse by the various seedlings of the wild hop from Italy has been constant for the particular plant year after year; in no single case has a seedling which was immune one season in the greenhouse shown susceptibility in other seasons in the greenhouse, although it may have done so in the hop-garden. The case has been very different with a seedling of American ancestry. This seedling was raised at Wye of the parentage (Oregon Cluster × English male hop) × English male hop[1]. In 1916 as a 2-year-old plant it proved throughout the season in the greenhouse persistently immune, in spite of the most numerous

[1] The "Oregon Cluster" is a commercial variety cultivated in the United States. In our opinion (see *Journal of Botany*, May 1915) it belongs to the species *Humulus americanus*, and not to *H. Lupulus*, from which the varieties cultivated in Europe derive their origin. The seedling now mentioned must therefore be considered of hybrid origin.

inoculations under conditions in which some hundreds of hop-seedlings of the same age became infected. The plant grew during that season to a height of 4 ft. In 1917 this seedling, which was still kept in the greenhouse, entirely lost its immunity. On April 19 there were small but "powdery" patches of mildew on four of its leaves. The leaves were at this date slightly yellowish, as the result of abnormal weather conditions, viz. rapid changes of temperature[1]. By May 9 the stem of the plant, after having been more or less completely checked in growth, was still growing only very slowly; there were now a few, fairly large "powdery" patches of mildew on four of the (upper) leaves. By May 22 the two stems of the plant were only 8 in. high, and still only lengthening slowly; the plant was clearly highly susceptible; the surface of the stem near its apex was covered all round, for a length of $1\frac{1}{2}$ in., with a continuous growth of the "powdery" conidial stage; several of the young leaves also were infected; and one of the stems had the terminal bud and the two youngest leaves smothered over with mildew and more or less hypertrophied. The plant, which as the result apparently of the severe attacks of mildew never made any very strong growth, reached a height of 2 ft. 10 in. Mildew persisted on it throughout the growing season. This seedling unfortunately died during the winter of 1917–18. It is to be noted that under these same cultural conditions in the greenhouse during 1917 the immune seedlings of the wild hop from Italy all retained their immunity.

We may ask here what is the explanation of the apparent change from immunity to susceptibility when a plant of Group 3 is transferred from the greenhouse to the hop-garden, and, conversely, of the change from susceptibility to immunity when the plant is brought back from the hop-garden to the greenhouse. The explanation may be sought for in two directions.

It is possible that there are different strains of the biologic form of *S. Humuli* on the hop with different powers of infection, and that the plant when in the hop-garden is attacked by a form which is absent in the greenhouse. The work of Barrus (4) would seem to give evidence of the existence of different strains of a parasitic fungus which are regional in their distribution. Whether such is the case with the Hop-mildew I hope to prove next year by inoculating the same (immune) plant in the greenhouse with spores taken from the same (susceptible) plant in the hop-garden.

[1] The conditions of growth at the time are described more fully in (2), p. 84.

On the other hand, the difference may well be not in the fungus but in the plant, which may change its power of resistance as the result of changed conditions of growth. The chief differences between the conditions in the hop-garden and in the greenhouse are the greater atmospheric humidity and (particularly towards the end of summer) the greater variation of temperature in the hop-garden, and the higher temperature reached in the greenhouse. It is noteworthy that the infection of the "immune" seedlings in the hop-garden is most evident in the autumn when low temperatures[1] occur at night. As regards the effect of greenhouse conditions, the statement has been made by Butler (5), p. 124, that "the mere growth of a plant under glass may reduce its resistance. Several varieties of wheat are much less resistant to black rust when grown in greenhouses than in the open, and the same is true of some other rusts and mildews." Butler (5), p. 162, also attributes the change from immunity to susceptibility sometimes shown by Einkorn wheat in India to the effect of high temperature. In the case of these hop seedlings, their transference to a higher temperature is associated, apparently, with a change to immunity.

SUMMARY.

1. Certain seedlings of the wild hop when grown in the greenhouse are persistently immune to the attacks of the mildew *Sphaerotheca Humuli*. This immunity has been shown by the same individual seedling for three consecutive years. Under the same cultural conditions other seedlings of the same parentage prove to be very susceptible.

2. Certain seedlings (Group 2) which are immune when grown in the greenhouse are also immune when grown in the open. These seedlings have retained this immunity after four years' residence in a hop-garden under normal conditions of cultivation and manuring.

3. Certain seedlings (Group 3) which are immune when grown in the greenhouse are susceptible when grown in the hop-garden; in some cases the susceptibility shown is of the highest grade.

4. "Cuts" taken from the seedlings of Group 3 in the same year in which the seedling proved to be susceptible in the hop-garden are immune in the greenhouse under cultural conditions in which "cuts" taken from other susceptible seedlings in the hop-garden are very susceptible.

[1] It is possible that the low temperature increases the infection-powers of the conidia of the mildew. In the *Erysiphaceae*, as in the *Uredineae*, "chilled" spores have increased powers of germination.

5. Certain seedlings (Group 4) are semi-immune to the attacks of the mildew.

6. One seedling (of American ancestry) grown in the greenhouse was immune throughout the season in 1916 and very susceptible in 1917.

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A LIST OF COCCIDAE AFFECTING VARIOUS GENERA OF PLANTS.

By E. ERNEST GREEN, F.E.S., F.Z.S.

(*Continued from Vol. V, page* 156)

QUERCUS (Fagaceae) 'Oak.'
- Monophlebus fuscipennis.
- Drosicha corpulenta.
- Icerya purchasi.
- Xylococcus quercus, napiformis.
- Kuwania quercus.
- Sphaerococcus sylvestris.
- Asterolecanium bornmuelleri, ilicicola, quercicola, variolosum, variolosum-minor, pasaniae.
- Lecaniodiaspis quercus, tessellata.
- Cerococcus corticis, ehrhorni, quercus.
- Nidularia pulvinata, japonica.
- Olliffiella cristicola.
- Kermes andrei, arizonensis, austini, ballotae, boguei, ceriferus, cockerelli, concinnulus, fuscus, galliformis, galliformis-cueroensis, gibbosus, gillettei, grandis, ilicis, kingii, nakagawae, nawae, nigropunctatus, nivalis, pallidus, perryi, pettiti, pubescens, quercus, roboris, trinotatus, variegatus-corticalis, vermilio, rattani, himalayensis, bacciformis, miyasakii, vastus, shastensis, mirabilis, branigani, cordiformis, essigii, lindingeri, occidentalis, sassceri, waldeni.
- Eriococcus quercus, howardi, quercus-gilensis, aceris.
- Phenacoccus quercus, aceris.
- Ceroputo koebelei.
- Pseudococcus quercus, agrifoliae, maritimus, quercicolus.
- Trionymus villosus.
- Lecanium antennatum, canadense, cerasifex, ciliatum, cockerelli, fuscum, lymani, pubescens, quercifex, quercitronis, emerici, nigrofasciatum, coryli, pulchrum.
- Pulvinaria innumerabilis, sericea, vitis.
- Diaspis montana.
- Protodiaspis parvula, agrifoliae.
- Chionaspis planchonii, quercus, chinensis, kinshinensis, salicis.
- Aspidiotus ancylus, cryptoxanthus, hederae, jordani, minimus, osborni, ostreaeformis, zonatus, lilacinus, obscurus, setiger, densiflorae, yulupae, vitis-suberi, distincta, alni, niger, pseudospinosus, tenebricosus, camelliae.
- Lepidosaphes citricola, crawii, ulmi.

QUINARIA (Vitaceae).
- Aspidiotus hederae.
- Lepidosaphes ulmi.

RADIOLA (Linaceae).
- Ripersia halophila.

RAMONA (Labiatae).
- Phenacoccus ramonae.
- Pseudococcus crawi.
- Puto yuccae.

RAPANEA (Myrsinaceae).
- Eriococcus corneus.
- Ceroplastes floridensis.

RAPHIA (Palmaceae).
- Ceroplastes actiniformis.
- Fiorinia macroprocta.

RAUWOLFIA (Apocynaceae).
  Lecanium hemisphaericum.
  Pulvinaria psidii.
RHAGODIA (Chenopodiaceae).
  Pulvinaria maskelli.
RHAMNUS (Rhamnaceae) 'Buckthorn.'
  Kermes nawae.
  Eriococcus gurneyi.
  Pseudococcus alaterni, citri.
  Tachardia lacca.
  Lecanium kunoensis, oleae, ciliatum, corni.
  Chionaspis salicis, furfura-fulva.
  Aspidiotus camelliae, britannicus, ostreaeformis, perniciosus.
  Parlatoria oleae.
  Lepidosaphes ulmi.
RHEEDIA (Clusiaceae).
  Asterolecanium aureum.
  Lecanium hemisphaericum, oleae.
  Aspidiotus dictyospermi.
RHEUM (Polygonaceae).
  Pseudococcus citrophilus.
RHINOCARPUS (Anacardiaceae).
  Aspidiotus rossi.
RHIPOGONUM (Liliaceae).
  Coelostomidia zealandica.
  Hemichionaspis minor.
  Lepidosaphes pyriformis.
RHIZOPHORA (Rhizophoraceae) 'Mangrove.'
  Lecanium rhizophorae, expansum-rotundum.
  Ctenochiton rhizophorae.
  Hemichionaspis congregabilis.
  Poliaspis lanigera.
  Aspidiotus rhizophorae, fissidens-constricta.
RHODODENDRON (Ericaceae).
  Eriococcus azaleae, bezzii, uvae-ursi.
  Hemichionaspis rhododendri.
  Aspidiotus duplex, paeoniae, rhododendri, ficus.
RHODOMYRTUS (Myrtaceae).
  Eriococcus rhodomyrti.
RHUS (Anacardiaceae).
  Pseudococcus quaintancei, capensis.
  Phenacoccus pettiti, stachyos.
  Lecanium robiniae-subsimile.
  Pulvinaria hazeae, maclurae, rhois.
  Ericerus pela.
  Takahashia jaliscensis.
  Chionaspis platani, mytilaspiformis.
  Aspidiotus perniciosus, duplex, africanus, pectinatus.
RHYNCHOSPERMUM (Compositae).
  Protopulvinaria pyriformis.
  Diaspis pentagona.
  Aspidiotus ficus.
RIBES (Grossulariaceae) 'Currant,' etc.
  Icerya purchasi.
  Pseudococcus arecae, gahani.
  Phenacoccus socius, aceris.
  Lecanium corni, coryli, rehi, ribis, websteri, nigrofasciatum.
  Pulvinaria occidentalis, vitis, betulae.
  Diaspis pentagona.
  Chionaspis furfurus, salicis.
  Epidiaspis piricola, lepèrei.
  Aspidiotus ancylus, forbesi, hederae, hunteri, perniciosus, tasmaniae, ostreaeformis, lataniae.
  Lepidosaphes ulmi.
RICHARDIA (Araceae).
  Pseudococcus capensis.
  Pulvinaria psidii.
RICINUS (Euphorbiaceae) 'Castor-oil.'
  Icerya purchasi.
  Lecanium hemisphaericum.
  Pulvinaria floccifera.
  Diaspis pentagona.
  Chionaspis eugeniae.
  Aspidiotus destructor, orientalis.
RINORIA (Violaceae).
  Aspidiotus sylvaticus.
ROBINIA (Leguminaceae).
  Gueriniella serratulae.
  Pseudococcus capensis, adonidum.
  Phenacoccus hystrix.
  Heliococcus bohemicus.
  Lecanium quadrifasciatum, quercitronis, robiniarum, robiniae, vini, corni, capreae, persicae.
  Pulvinaria innumerabilis.
  Aspidiotus juglans-regiae, africanus, rapax, hederae.
  Parlatoria oleae.

RODRIGUESIA (Orchidaceae).
CONCHASPIS angraeci.
ROLLINIA (Anonaceae).
PALAEOCOCCUS rosae.
ROSA (Rosaceae).
ICERYA purchasi, seychellarum, aegyptiaca.
PALAEOCOCCUS rosae.
ORTHEZIA insignis.
TACHARDIA rosae.
LECANIUM perornatum, rosae, persicae, oleae, pulchrum, coryli, corni, nigrofasciatum.
PULVINARIA coulteri, betulae.
DIASPIS rosae.
CHIONASPIS salicis.
ASPIDIOTUS ficus, aurantii, dictyospermi, articulatus, orientalis, perniciosus, lataniae, tesserata, hederae, camelliae.
LEPIDOSAPHES ulmi.
PARLATORIA calianthina, proteus, oleae.
ROSIMARINUS (Labiatae) 'Rosemary.'
ICERYA purchasi.
ERIUM rorismarinus.
LECANIUM oleae, corni.
RUBIA (Rubiaceae).
ASPIDIOTUS hederae.
RUBUS (Rosaceae).
ORTHEZIA urticae.
ERIOCOCCUS multispinus.
PSEUDOCOCCUS glaucus.
PHENACOCCUS rubivorus, colemani, comari.
TETRURA rubi.
LECANIUM coryli, fitchii, obtusum, rubi, pulchrum, hesperidum, corni, capreae, persicae.
PULVINARIA vitis.
DIASPIS rosae.
CHIONASPIS dubia.
ASPIDIOTUS perniciosus.
LEPIDOSAPHES ulmi.
RUMEX (Polygonaceae).
ICERYA purchasi.
ERIOCOCCUS insignis.
PSEUDOCOCCUS arecae, capensis.
RIPERSIELLA rumicis.
RUSCUS (Liliaceae).
CEROPLASTES rusci.
ASPIDIOTUS britannicus, hederae.
FIORINIA pellucida.
RUTA (Rutaceae).
CHIONASPIS canariensis, berlesii.

SABAL (Palmaceae).
COMSTOCKIELLA sabalis.
ASPIDIOTUS personatus, pseudospinosus, dictyospermi.
ISCHNASPIS filiformis.
SACCHARUM (Gramineae) 'Sugar-Cane.'
ICERYA seychellarum.
MARGARODES formicarium.
PSEUDOCOCCUS calceolariae, sacchari, saccharifolii, boninsis, virgatus.
RIPERSIA sacchari.
LECANIUM guerinii.
PULVINARIA iceryi, elongata.
DIASPIS major.
CHIONASPIS depressa, madiunensis, saccharifolii.
ASPIDIOTUS sacchari, glomeratus, destructor.
SAGITTARIA (Alismaceae).
PSEUDOCOCCUS virgatus.
SAGUERUS (Palmaceae).
ASPIDIOTUS spinosus.
SALICORNIA (Chenopodiaceae).
CEROPUTO ambigua.
PULVINARIA salicorniae.
SALIX (Salicaceae) 'Willow,' 'Sallow,' etc.
ICERYA purchasi.
ERIOCOCCUS borealis.
PHENACOCCUS aceris.
LECANIUM nigrofasciatum, coryli, corni, ciliatum.
PULVINARIA ehrhorni, innumerabilis, occidentalis, vitis, betulae.
DIASPIS pentagona.
CHIONASPIS lintneri, ortholobis, salicis, salicis-nigrae, wistariae.
HEMICHIONASPIS minor.
HOWARDIA biclavis.
LEUCASPIS kermanensis, salicis.

SALIX (Salicaceae)—*cont.*
- Aspidiotus ancylus-serratus, perniciosus, camelliae, aurantii, distincta, ostreaeformis, lataniae, alienus, pectinatus.
- Lepidosaphes pallida, ulmi.

SALSOLA (Chenopodiaceae).
- Chionaspis canariensis, berlesei.

SALVIA (Labiatae).
- Orthezia insignis.
- Cerococcus zapotlana.
- Pseudococcus crawii, transvaalensis.

SAMBUCUS (Caprifoliaceae) 'Elder.'
- Asterolecanium pustulans-sambuci, fimbriatum.
- Pseudococcus obscurus, bakeri.

SAMOLUS (Primulaceae).
- Asterolecanium stypheliae-multiporum.

SANCHEZIA (Acanthaceae).
- Orthezia praelonga.

SANDORICUM (Meliaceae).
- Pinnaspis siphonodontis.

SANGUISORBA (Rosaceae).
- Margarodes polonicus.
- Asterolecanium fimbriatum.

SANICULA (Umbelliferae).
- Asterolecanium fimbriatum.

SANTALUM (Santalaceae) 'Sandalwood.'
- Rhizococcus fossor.
- Pseudococcus gallicola.
- Inglisia foraminifer.
- Diaspis santali.
- Poliaspis exocarpi.
- Aspidiotus santali.

SAPINDUS (Sapindaceae).
- Lecanium gracilis, tessellatum, nigrofasciatum.
- Diaspis ceylonica.
- Howardia biclavis.
- Fiorinia nephelii, sapindi.

SAPOTA (Sapotaceae).
- Icerya purchasi.
- Lecanium mangiferae, nanus, tessellatum, oleae.
- Pulvinaria psidii.
- Protopulvinaria pyriformis.
- Diaspis persimilis, miranda.

SAPROSMA (Rubiaceae).
- Aspidiotus transparens.
- Fiorinia rubrolineata, saprosmae.
- Parlatoria mytilaspiformis.

SAROTHAMNUS (Leguminosae).
- Lecanium pulchrum, coryli, corni.
- Pulvinaria betulae.
- Chionaspis salicis.
- Aspidiotus hederae.
- Lepidosaphes ulmi.

SASSAFRAS (Lauraceae).
- Lecanium lintneri.
- Lepidosaphes ulmi.

SAUVAGESIA (Ochnaceae).
- Ceroplastes ceriferus.

SAXEGOTHAEA (Coniferae).
- Pseudoparlatoria chilina.

SAXIFRAGA (Saxifragaceae).
- Orthezia cataphracta.
- Aspidiotus hederae, dictyospermi.

SCAEVOLA (Goodenovieae).
- Lecanium tessellatum.

SCALESIA (Compositae).
- Orthezia galapagoensis.
- Aspidiotus lataniae.

SCHINUS (Anacardiaceae).
- Lecanium hemisphaericum, nigrum.
- Pulvinaria psidii.
- Ceroplastes albolineatus, cistudiformis, rusci, sinensis, postperlucidus.
- Hemichionaspis aspidistrae.
- Aspidiotus africanus.

SCHIZOSTACHYUM (Gramineae).
- Asterolecanium miliaris-longum.
- Odonaspis schizostachyi.

SCHLEICHERA (Sapindaceae).
- Monophlebus stebbingi.
- Tachardia lacca, albizziae.

SCHOTIA (Leguminosae).
- Aonidia biafrae.

SCIADOPYTIS (Coniferae).
- Pseudococcus ryani.
- Lepidosaphes newsteadi.

SCLERANTHUS (Caryophyllaceae).
- Margarodes polonicus.

SCOLOPENDRIUM (Filices).
- Lecanium hesperidum.

SCOLOPIA (Bixaceae).
- Parlatoria cingala.

SCORPIURUS (Leguminosae).
ASTEROLECANIUM fimbriatum.
SCROPHULARIA (Scrophulariaceae).
ASTEROLECANIUM fimbriatum.
CEROPUTO superbus.
SEAFORTHIA (Palmaceae).
DIASPIS boisduvali.
ASPIDIOTUS ficus.
PARLATORIA pergandei.
SEDUM (Crassulaceae).
ICERYA purchasi.
DIASPIS pentagona.
ASPIDIOTUS hederae, camelliae.
SELENIPEDIUM (Orchidaceae).
PARLATORIA proteus.
SEMELE (Liliaceae).
ASPIDIOTUS lauretorum.
SEMPERVIVUM (Crassulaceae).
ASPIDIOTUS hederae.
SENEBIERA (Cruciferae).
PSEUDOCOCCUS capensis.
SENECIO (Compositae).
PSEUDOCOCCUS capensis, adonidum.
LECANIUM hemisphaericum.
ASPIDIOTUS niger.
SEQUOIA (Coniferae).
PSEUDOCOCCUS sequoiae.
PUTO cupressi.
DIASPIS visci.
ASPIDIOTUS coniferarum.
SERRATULA (Compositae).
GUERINIELLA serratulae.
LECANIUM pulchrum.
SESBANIA (Leguminosae).
LECANIUM discrepans, oleae.
SHOREA (Dipterocarpaceae).
TACHARDIA lacca.
SIDA (Malvaceae).
ASTEROLECANIUM pustulans.
PSEUDOCOCCUS burnerae, virgatus.
PHENACOCCUS insolitus.
LECANIUM nigrum.
CHIONASPIS solani.
HEMICHIONASPIS minor.
SIDEROXYLON (Sapotaceae).
LECANIUM sideroxylium.
DIASPIS persimilis.
ASPIDIOTUS fissidens-pluridentatus.
SILENE (Caryophyllaceae).
PSEUDOCOCCUS capensis.
SIPHONODON (Celastraceae).
NEOLECANIUM cribrigerum.
PINNASPIS siphonodontis.
SMILAX (Liliaceae).
ICERYA purchasi.
LECANIUM urichi.
PULVINARIA convexa.
FILIPPIA oleae.
DIASPIS rosae-spinosa.
ASPIDIOTUS smilacis, lauretorum, britannicus, hederae, rossi.
LEPIDOSAPHES cocculi.
SOJA (Leguminosae) 'Soya Bean.'
ERIOCOCCUS sojae.
SOLANDRA (Solanaceae).
PSEUDOCOCCUS citri.
SOLANUM (Solanaceae).
ICERYA purchasi.
CEROCOCCUS hibisci.
PSEUDOCOCCUS affinis, citri, solani, secretus, capensis, virgatus, citrophilus, corymbatus.
PHENACOCCUS insolitus, stachyos, solani.
LECANIUM pseudosemen, tolucanum, hemisphaericum, oleae.
MESOLECANIUM lucidum.
PULVINARIA floccifera, psidii.
CEROPLASTES cirripediformis.
INGLISIA castilloae.
DIASPIS pentagona.
CHIONASPIS manni, solani.
HOWARDIA biclavis.
ASPIDIOTUS cydoniae, orientalis, camelliae.
LEPIDOSAPHES alba.
SOLDANELLA (Primulaceae).
ORTHEZIA cataphracta.
SOLENOPSIS (Campanulaceae).
PHENACOCCUS solenopsis.
SOLIDAGO (Compositae).
ICERYA purchasi.
ORTHEZIA solidaginis, urticae.
SONCHUS (Compositae).
ICERYA purchasi.
PSEUDOCOCCUS capensis.
SONERILA (Melastomaceae).
LECANIUM hesperidum.

SOPHORA (Leguminosae).
Diaspis texensis, pentagona.
Chionaspis salicis.
Aspidiotus sophorae.
SORBUS (Rosaceae).
Lepidosaphes ulmi.
SORGHUM (Gramineae) 'Millet.'
Pseudococcus sorghiellus, sorghiellus-kingi.
SPARTINA (Gramineae).
Ripersiella maritima.
Chionaspis spartinae.
SPARTIUM (Leguminosae).
Icerya purchasi.
Asterolecanium algeriense, fimbriatum.
Lecanium mori.
Aspidiotus hederae.
Lepidosaphes ulmi.
SPARTOCYTISUS (Leguminosae).
Aspidiotus lataniae.
Lepidosaphes ulmi.
SPERGULA (Caryophyllaceae).
Pseudococcus capensis.
SPERGULARIA (Caryophyllaceae).
Margarodes polonicus.
Pseudococcus calceolariae, luffi.
SPHAGNUM (Lycopodiaceae).
Orthezia cataphracta.
Newsteadia floccosa.
Pseudococcus sphagni, perrisii.
SPIRAEA (Rosaceae).
Lecanium vini, websteri, corni, persicae.
Pulvinaria cockerelli, vitis.
Lichtensia viburni.
Aspidiotus perniciosus, hederae.
Lepidosaphes ulmi.
SPONDIAS (Anacardiaceae).
Llaveia axin.
Pseudococcus virgatus.
Pulvinaria psidii.
Aspidiotus subsimilis-anonae.
SPOROBOLUS (Gramineae).
Ripersia sporoboli.
Aclerda obscura.
STACHYS (Labiatae).
Icerya purchasi.
Asterolecanium fimbriatum.
Pseudococcus eriogoni.
Phenacoccus stachyos.
Puto yuccae.
Lecanium pulchrum.
Aspidiotus labiatarum.
STANGERIA (Cycadaceae).
Pseudococcus longispinus.
Lecanium hemisphaericum.
STAPELIA (Asclepiadaceae).
Aspidiotus hederae.
STAPHYLEA (Staphylaceae).
Aspidiotus ancylus.
STATICE (Plumbaginaceae).
Ripersia halophila.
Lecanium hesperidum, hemisphaericum.
STELLARIA (Caryophyllaceae).
Orthezia urticae.
STEPHANOTIS (Asclepiadaceae).
Conchaspis angraeci.
Ripersia terrestris.
Aspidiotus destructor.
STERCULIA (Sterculiaceae).
Lecanium hesperidum.
Hemichionaspis minor.
STEREOSPERMUM (Bignoniaceae).
Cribrolecanium formicarum.
STILLINGIA (Euphorbiaceae).
Lecanium globulosum.
Lepidosaphes ulmi.
STRAUSSIA (Rubiaceae).
Pseudococcus straussiae.
STREBLUS (Urticaceae).
Tachardia lacca.
STRELITZIA (Musaceae).
Ceroplastes rusci.
Diaspis boisduvalli.
Aspidiotus dictyospermi, ficus, camelliae.
Fiorinia fioriniae, pellucida.
STROBILANTHES (Acanthaceae).
Orthezia insignis.
Pedronia strobilanthis.
Chionaspis strobilanthi.
Hemichionaspis aspidistrae.
Aspidiotus putearius.
STROMBOSIOPSIS (Olaeaceae).
Aspidiotus spiniger.

STRYCHNOS (Loganiaceae).
Lecanium viride.
Pulvinaria psidii.
Diaspis stilosa.
Aspidiotus fissidens, undulatus.
Ischnaspis bipindensis.
STYPHELIA (Epacridaceae).
Asterolecanium stypheliae.
Sphaerococcus stypheliae.
Ctenochiton serratum.
Aspidiotus immaculatus.
SWIETENIA (Meliaceae) 'Mahogany' etc.
Aspidiotus orientalis.
SYMPHORICARPUS (Caprifoliaceae).
Phenacoccus colemani.
Lecanium corni.
Pulvinaria betulae.
SYMPLOCOS (Symplocaceae).
Eriococcus japonicus.
Cerococcus albospicatus.
SYNCARPIA (Myrtaceae).
Gossyparia syncarpiae.
SYNGONIUM (Araceae).
Hemichionaspis aspidistrae.
SYRINGA (Oleaceae) 'Lilac.'
Pseudococcus syringae.
Lecanium corni.
Pulvinaria innumerabilis, vitis.
Diaspis pentagona.
Chionaspis salicis.
Aspidiotus diffinis, perniciosus, hederae, pectinatus.
Lepidosaphes ulmi.
SYZYGIUM (Myrtaceae).
Diaspis africana.
Lepidosaphes ungulata.

TABERNAEMONTANA (Apocynaceae).
Margarodes rileyi.
Lecanium tessellatum, hemisphaericum, hesperidum, viride.
Ceroplastes roseatus.
Conchaspis angraeci.
Howardia biclavis.
Aonidia cornigera.
TALINUM (Portulaccaceae).
Pseudococcus virgatus.
Lecanium hesperidum.
TAMARINDUS (Leguminaceae).
Monophlebus tamarindus.
Margarodes rileyi.
Tachardia lacca.
Lecanium oleae.
Chionaspis acuminata.
Hemichionaspis minor.
Howardia biclavis.
Aspidiotus lataniae, tamarindi, orientalis.
TAMARIX (Tamaricaceae).
Monophlebus tamarindus.
Gossyparia mannifera.
Erium lichtensioides.
Puto africanus.
Lecanium oleae, hemisphaericum.
Pulvinaria psidii.
Trabutina elastica.
Chionaspis etrusca.
Adiscodiaspis tamaricola.
TARAXACUM (Compositae).
Orthezia urticae.
TAXUS (Coniferae) 'Yew.'
Pseudococcus kraunhiae, taxi.
Pulvinaria floccifera.
Diaspis taxicola.
Aspidiotus taxus, aurantii.
Fiorinia odinae-multipora.
Lepidosaphes citricola.
TECOMA (Bignoniaceae).
Lecanium somereni, corni, persicae, viride.
Pulvinaria psidii.
Howardia biclavis.
Aspidiotus hederae.
TECTONA (Verbenaceae) 'Teak.'
Monophlebus tectonae.
Icerya sulfurea-pattersoni.
Lecanium nigrum.
Pulvinaria psidii.
TEINOSTACHYUM (Gramineae).
Antonina zonata.
TELOPEA (Proteaceae).
Chionaspis eugeniae.
TEMPLETONIA (Leguminosae).
Asterolecanium fimbriatum.
Aspidiotus ceratus.
Lepidosaphes chitinosa.

TEPHROSIA (Leguminaceae).
Cerococcus hibisci.
Pseudococcus virgatus.
Phenacoccus iceryoides.
Aspidiotus orientalis.
TERMINALIA (Combretaceae).
Pseudococcus crotonis.
Lecanium terminaliae, begoniae, nigrum, oleae.
Howardia biclavis.
Aspidiotus destructor, ficus.
TETRANTHERA (Lauraceae).
Chionaspis minuta, megaloba.
TETRASTIGMA (Vitaceae).
Lecanium luzonicum.
TEUCRIUM (Labiatae).
Orthezia delavauxii, urticae.
Asterolecanium fimbriatum.
Aspidiotus labiatarum.
THEA (Ternstromiaceae) 'Tea.'
Icerya aegyptiaca, purchasi.
Margarodes rileyi.
Orthezia insignis.
Tachardia decorella, decorella-theae.
Cerococcus ficoides.
Pseudococcus citri, theaecola.
Phenacoccus ornatus.
Ripersia theae.
Lecanium notatum, viride, watti, formicarii, discrepans, nigrum, hemisphaericum, colemani.
Pulvinaria aurantii, psidii, theae.
Lichtensia japonica.
Ceronema japonica.
Eriochiton theae.
Ceroplastes ceriferus, floridensis, rubens.
Diaspis pentagona-theae.
Chionaspis manni, caroli.
Hemichionaspis separata, theae, aspidistrae.
Howardia biclavis.
Fiorinia fioriniae, theae.
Aspidiotus camelliae, cyanophylli, destructor, dictyospermi, theae, lataniae, orientalis, duplex, poeoniae, transparens.
Lepidosaphes newsteadi.
Parlatoria theae, mytilaspiformis, sylvaticus.
THEOBROMA (Sterculiaceae) 'Cacao.'
Palaeococcus theobromae.
Asterolecanium pustulans.
Tachardia albizziae.
Pseudococcus theobromae, crotonis, citri, tayabanus, virgatus.
Stictococcus sjostedti, dimorphus, gowdeyi, intermedius.
Hemilecanium theobromae.
Pulvinaria jacksoni.
Ceroplastes bussei, theobromae.
Ceroplastodes virescens.
Inglisia conchiformis, theobromae.
Philephedra broadwayi.
Aspidiotus trilobitiformis, palmae, articulatus.
Pseudoparlatoria pusilla.
THEOPHRASTA (Myrsinaceae).
Pulvinaria psidii.
THESIUM (Santalaceae).
Asterolecanium fimbriatum, thesii.
THESPESIA (Malvaceae).
Palaeococcus bicolor.
Walkeriana cinerea.
Asterolecanium thespesiae.
Lecanium nigrum.
Pulvinaria thespesiae.
Inglisia bivalvata.
Pseudococcus corymbatus.
Phenacoccus glomeratus.
THRINAX (Palmaceae).
Diaspis trinacis, boisduvali.
Chionaspis unilateralis.
Pinnaspis buxi.
Aspidiotus destructor.
THUJA (Coniferae).
Pseudococcus ryani.
Lecanium fletcheri, arion.
Diaspis carueli, minima, visci.
Chionaspis striata.
Aspidiotus lataniae, hederae.
Parlatoria chinensis.
THUNBERGIA (Acanthaceae).
Orthezia insignis.
Pseudococcus virgatus.
Ceroputo barberi.
Hemichionaspis minor.

THUNBERGIA (Acanthaceae)—*cont.*
ASPIDIOTUS dictyospermi, lataniae.
PARLATORIA pergandei.
THYMELAEA (Thymelaeaceae).
ERIOCOCCUS thymelaeae.
ASPIDIOTUS privignus, labiatarum, hederae, niger.
THYMUS (Labiatae).
ERIOCOCCUS ericae.
LECANIUM oleae.
TILIA (Tiliaceae) 'Lime.'
XYLOCOCCUS filiferus.
PHENACOCCUS aceris, acericola.
LECANIUM nigrofasciatum, tulipiferae, coryli.
PULVINARIA innumerabilis, tiliae, vitis.
CHIONASPIS salicis.
ASPIDIOTUS ancylus, diffinis, ostreaeformis, perniciosus.
LEPIDOSAPHES ulmi.
TILLANDSIA (Bromeliaceae).
ASPIDIOTUS personatus.
TOLPIS (Compositae).
ASPIDIOTUS rapax.
TORREYA (Coniferae).
PUTO cupressi.
POLIASPIS pini.
TOWNSENDIA (Compositae).
PALAEOCOCCUS townsendi.
TRACHYCARPUS (Palmaceae).
LECANIUM tessellatum.
ASPIDIOTUS persearum, hederae.
PARLATORIA pergandei.
TRACHYMENA (Umbelliferae).
ERIOCOCCUS buxi-australis.
TRECULIA (Artocarpaceae).
LECANIUM longulum.
TREMA (Urticaceae).
ANOMALOCOCCUS cremastogastri.
LECANIUM tremae.
DIASPIS pentagona.
TRIBULUS (Zygophyllaceae).
PSEUDOCOCCUS virgatus-humilis.
TRICALYSIA (Cinchonaceae).
ASPIDIOTUS gracilis.
TRICHILIA (Meliaceae).
PSEUDOCOCCUS trichiliae.
TRICHOGONIA (Compositae).
TECTOPULVINARIA albata.
TRICHOMANES (Filices).
RIPERSIA filicicola.
TRICYCLA (Nyctaginaceae).
CEROCOCCUS andinus.
TRIFOLIUM (Leguminaceae).
GUERINIELLA serratulae.
ORTHEZIA urticae.
ASTEROLECANIUM fimbriatum.
PSEUDOCOCCUS trifolii, aridorum.
LECANIUM tulipiferae.
ASPIDIOTUS hederae.
TRIPLARIS (Polygonaceae).
CEROPLASTES floridensis.
TRISTANIA (Myrtaceae).
ASPIDIOTUS subrubescens.
TRITICUM (Gramineae).
ERIOCOCCUS insignis.
PHENACOCCUS cholodkovskyi, graminis.
MICROCOCCUS similis.
TRIUMFETTA (Tiliaceae).
HEMICHIONASPIS minor.
TROPHIS (Artocarpaceae).
ASPIDIOTUS tesseratus.
TSUGA (Coniferae).
PHYSOKERMES taxifoliae.
LEUCASPIS kelloggi.
ASPIDIOTUS tsugae, ehrhorni, abietis.
TULIPA (Liliaceae).
PSEUDOCOCCUS hibernicus.
TUNICA (Caryophyllaceae).
ORTHEZIA urticae.
TUPIDANTHUS (Araliaceae).
PSEUDOCOCCUS adonidum.
TURPINIA (Sapindaceae).
AONIDIA columnifera.
FIORINIA fioriniae.
TURRAEA (Meliaceae).
HEMICHIONASPIS chionaspiformis.
TYLOPHORA (Asclepiadaceae).
DIASPIS pentagona.

ULEX (Leguminosae) 'Gorse.'
ICERYA purchasi.
ERIOCOCCUS insignis.
PHENACOCCUS aceris.
LECANIUM mori, pulchrum.
ASPIDIOTUS camelliae, hederae.
LEPIDOSAPHES ulmi-ulicis.

ULMUS (Ulmaceae) 'Elm.'
Gueriniella serratulae.
Lecaniodiaspis pruinosa.
Gossyparia spuria.
Pseudococcus adonidum, citri, longispinus.
Phenacoccus ulmi, aceris.
Ripersia pupifera.
Lecanium aceris, canadense, caryae, cockerelli, quercitronis, corni, rugosum, tiliae, nigrofasciatum, coryli, capreae.
Pulvinaria innumerabilis, pruni, vitis.
Diaspis pentagona.
Chionaspis americana, furfura, salicis.
Aspidiotus perniciosus, ulmi, ostreaeformis, camelliae, cydoniae, hederae.
Lepidosaphes ulmi, ficifoliae-ulmicola.
UNCARIA (Rubiaceae).
Hemichionaspis aspidistrae.
URENA (Malvaceae).
Diaspis pentagona.
Hemichionaspis minor.
URERA (Urticaceae).
Phyllococcus oahuensis.
URTICA (Urticaceae) 'Nettle.'
Icerya purchasi.
Orthezia urticae.
Pseudococcus citri.
Diaspis pentagona.
UVARIA (Anonaceae).
Ceroplastes uvariae.
Hemichionaspis uvariae.

VACCINIUM (Ericaceae).
Eriococcus quercus, costaricensis.
Lecanium distinguendum, kingi, nigrofasciatum, websteri, coryli.
Pulvinaria ericae.
Chionaspis salicis.
Aspidiotus oxycoccus.
Lepidosaphes ulmi.
VALERIANODES (Verbenaceae).
Hemichionaspis minor.
VANDA (Orchidaceae).
Parlatoria pseudaspidiotus, proteus.
Lepidosaphes vandae.
VANILLA (Orchidaceae).
Aspidiotus aurantii.
VATERIA (Dipterocarpaceae).
Aonidia tentaculata.
Parlatoria vateriae.
VATICA (Dipterocarpaceae).
Ischnaspis spathulata.
VERBENA (Verbenaceae).
Palaeococcus nudatus.
Icerya purchasi.
Pseudococcus adonidum.
VERNONIA (Compositae).
Orthezia insignis.
Tectopulvinaria albata.
Ceroplastes novaesi.
Inglisia castilloae.
Howardia biclavis.
VERONICA (Scrophulariaceae).
Asterolecanium fimbriatum.
Pseudococcus alpinus.
Lecanium pulchrum.
Aspidiotus hederae.
Poliaspis media.
VERSCHAFFELTIA (Palmaceae).
Aonidia simplex.
VIBURNUM (Caprifoliaceae).
Cerococcus muratae.
Pseudococcus viburni, citri.
Phenacoccus aceris.
Lecanium corylifex, corni.
Pulvinaria innumerabilis, viburni, vitis.
Lichtensia viburni.
Filippia oleae.
Chionaspis lintneri, eugeniae, salicis.
Aspidiotus perniciosus, britannicus, hederae, spinosus, perseae.
Parlatoria myrtus.
Lepidosaphes ulmi.
VICIA (Leguminosae).
Gueriniella serratulae.
Asterolecanium fimbriatum.
VIMINARIA (Leguminosae).
Pulvinaria maskelli-viminariae.
VINCA (Apocynaceae).
Orthezia urticae.
Lecanium hesperidum, corni, oleae
Aspidiotus rapax, hederae, britannicus.

VIOLA (Violaceae).
PSEUDOCOCCUS virgatus, eriogoni.
PHENACOCCUS wilmattae.
VISCUM (Loranthaceae) 'Mistletoe.'
GOSSYPARIA spuria.
POROCOCCUS pergandei, tinctorius.
LECANIUM hesperidum.
PULVINARIA betulae.
CEROPLASTES rusci.
DIASPIS phoradendri, visci.
LEPIDOSAPHES ulmi.
VISNEA (Ternstromiaceae).
LECANIUM hemisphaericum.
ASPIDIOTUS lauretorum.
VITEX (Verbenaceae).
ASPIDIOTUS hederae.
VITIS (Vitaceae).
GUERINIELLA serratulae.
ICERYA purchasi, palmeri.
MARGARODES vitium, capensis, greeni.
PSEUDOCOCCUS subterraneus, longispinus, bakeri, capensis, citri, adonidum, vitis.
PHENACOCCUS aceris.
RHIZOECUS falcifer.
LECANIUM armeniacum, berberidis, vini, oleae, fukayi, magnoliarum, nigrofasciatum, persicae, longulum, corni, corni-robiniarum.
PULVINARIA innumerabilis, simplex, vinifera, vitis, betulae.
LICHTENSIA viburni.
CRYPTINGLISIA lounsburyi.
DIASPIS pentagona.
CHIONASPIS vitis.
HEMICHIONASPIS minor.
ASPIDIOTUS cydoniae, uvae, tesserata, aurantii, obscurus, vitis, fossor, convexus, pedroniformis, perniciosus, rapax, ficus, labiatarum, pectinatus, hederae.
LEPIDOSAPHES ulmi, ulmi-vitis, buzenensis.
PARLATORIA proteus, oleae, pergandei-camelliae.
VOACANGA (Apocynaceae).
PROTOPULVINARIA longivalvata-bakeri.
VRIESIA (Bromeliaceae).
ASPIDIOTUS hederae.

WACHENDORFIA (Liliaceae).
PSEUDOCOCCUS wachendorfiae.
WALSURA (Meliaceae).
AONIDIA dentata.
FIORINIA fioriniae.
WARNERIA (Rubiaceae).
PULVINARIA psidii.
PROTOPULVINARIA pyriformis.
WASHINGTONIA (Palmaceae).
LECANIUM hesperidum.
DIASPIS boisduvali.
COMSTOCKIELLA sabalis.
ASPIDIOTUS ficus.
PARLATORIA pergandei.
WENDLANDIA (Rubiaceae).
PHENACOCCUS iceryoides.
WENDTIA (Geraniaceae).
CEROCOCCUS badius.
WIGANDIA (Hydroleaceae).
ASPIDIOTUS lataniae.
LEPIDOSAPHES pinnaeformis.
WILLUGHBEIA (Apocynaceae).
ASPIDIOTUS javanensis.
WISTERIA (Leguminosae).
CONCHASPIS angraeci.
PSEUDOCOCCUS kraunhiae.
CHIONASPIS wisteriae.
ASPIDIOTUS perniciosus.
WITHAMIA (Solanaceae).
LECANIUM nigrum.

XANTHOPHYLLUM (Polygalaceae).
CRYPTOPARLATORIA parlatorioides.
XANTHORRHOEA (Liliaceae).
CHIONASPIS xanthorrhoeae.
ASPIDIOTUS rossi.
LEPIDOSAPHES pallens.
XANTHOSOMA (Araceae).
PSEUDOCOCCUS virgatus.
XANTHOXYLUM (Rutaceae).
LECANIUM quercitronis, infrequens, xanthoxylum.
CEROPLASTES grandis.
XEROTES (Juncaceae).
CHIONASPIS xerotidis.
ASPIDIOTUS cladii.

XIMENIA (Olacaceae).
  CHIONASPIS nigerensis.
XYLIA (Leguminosae).
  TACHARDIA lacca.
XYLOCARPUS (Meliaceae).
  CHIONASPIS usambarica.
  ASPIDIOTUS articulatus.
XYLOPHYLLA (Euphorbiaceae).
  ASPIDIOTUS lataniae.

YUCCA (Liliaceae).
  LECANIODIASPIS yuccae.
  PSEUDOCOCCUS olivaceus.
  CEROPUTO yuccae.
  LECANIUM oleae, hesperidum.
  CEROPLASTES rusci.
  CONCHASPIS angraeci.
  HEMICHIONASPIS minor.
  ASPIDIOTUS hederae, yuccae, yuccae-neomexicana, yuccarum, lataniae, biformis, alienus.
  LEPIDOSAPHES nigra, philococcus, ulmi.

ZALACCA (Palmaceae).
  ISCHNASPIS filiformis.
ZAMIA (Cycadaceae).
  PSEUDOCOCCUS zamiae.
  LECANIUM hemisphaericum.
  DIASPIS zamiae, pentagona.
  HEMICHIONASPIS minor.
  ASPIDIOTUS ficus.
ZANTEDESCHIA (Araceae).
  PULVINARIA psidii.
ZEA (Gramineae) 'Maize.'
  CEROPLASTES rusci.
  ASPIDIOTUS dictyospermi.
ZILLA (Cruciferae).
  ASPIDIOTUS seurati.
ZINGIBER (Zingiberaceae).
  CEROPLASTES rubens.
ZIZYPHUS (Rhamnaceae).
  TACHARDIA lacca.
  PSEUDOCOCCUS perniciosus, filamentosus.
  CEROPLASTODES cajani.
  PULVINARIA burkilli.
  DIASPIS pentagona.
  CHIONASPIS megaloba.
  ASPIDIOTUS lataniae.
  PARLATORIA zizyphi, chinensis.
ZUCCAGNIA (Leguminosae).
  ERIOCOCCUS diversispinus.
  LECANIUM silvestrii.

(*Note.* The names in the foregoing list have, in most cases, been entered in the exact form in which they have been recorded by the various observers. Consequently, the same species may sometimes appear under different aliases: e.g. *Pseudococcus adonidum* and *longispinus*; *Lecanium persicae, coryli* and *corni*; etc. I have left them as they are, partly because the synonymy is not yet universally accepted and, also, for the convenience of observers who would recognise the species more readily by the names to which they are accustomed.)

Some interesting observations on the host-affinities of *Coccidae* may be gathered from these lists. It will be noticed, for instance, that the GRAMINEAE (including the Bamboos) have a special Coccid fauna comprising such genera as *Antonina*, *Aclerda*, *Eriopeltis*, *Lecanopsis* and *Odonaspis*. The CONIFERAE have a monopoly of the genus *Physokermes* and support twelve out of the eighteen named species of *Leucaspis*. The genus *Kermes* is dependent upon species of Oak; while most of the gall-making Coccidae—including the genera *Opisthoscelis*, *Ascelis* and *Apiomorpha*—occur only upon various species of *Eucalyptus*.

The grasses can probably claim to support the largest number of species, with the total of 243, out of which number 63 must be credited to the Bamboos. Of individual genera, *Eucalyptus* heads the list, with 133 separate species; but is run very close by *Acacia* with 130 and *Quercus* with 124. If the *Acacias* and *Mimosas* were to be counted together, they would take the first place with a sum total of 149. The only other genus that exceeds the century is *Ficus*, with 102; though it is closely approached by *Citrus*, with 99. After these, the figures drop very steeply, *Pyrus* coming next with 59 species to its credit, followed by *Vitis* with 54, *Thea* and *Pinus* with 52 apiece, and *Cocos* with 48. The rest tail off very rapidly.

It would be interesting to ascertain the species of *Coccidae* that have the largest number of host-plants, but this would entail more labour than I should care to expend upon the work. I think, however, that *Pseudococcus citri*, *Lecanium hesperidum*, *Lepidosaphes ulmi* and *Aspidiotus hederae* would come somewhere near the top of the list.

THE USE OF SCIENTIFIC AND POPULAR NAMES IN ECONOMIC BIOLOGY.

By S. A. NEAVE, M.A., D.Sc. (Oxon.).

Biological science in its economic aspects is a comparatively modern study, and since it necessarily appeals to a far wider public than does the purely scientific side of the subject, it is perhaps not unnatural, and to some extent inevitable, that popular names for plants and animals should be widely used in preference to scientific ones by writers on the subject. At the same time it must be recognised that the work of the systematist is necessarily the foundation on which economic workers must build. Without the accurate identification and nomenclature of plants or animals, no important study of their biology or distribution can be rendered available to others and no comparison of results can be made between those who speak different languages.

It is obvious however that much of the work of the economic biologist is published for the benefit of agriculturists and others who have little or no scientific training. It is therefore essential that to convey anything to such a public the popular names of the plants and animals concerned must be used. This does not however justify the *omission* of scientific names, a practice that is only too frequent at the present time. If the use of these in the text is objected to, they can always be added as a footnote—as is done in many of the bulletins of the United States Department of Agriculture.

One objection—and that not an unreasonable one—that has been raised to the use of scientific names is the unfortunate change in nomenclature that continually arises, even in the case of the commonest species and most widely known pests. The recent change of the name of the brown-tail moth—known for so long as *Euproctis chrysorrhoea* and now called *Nygmia phaeorrhoea*—is a good example of this. Though this objection is sound so far as it goes, the remedy lies, not in the disuse of scientific names, but in the cooperation on the part of workers in the economic field to put pressure on the International Committee on Zoological Nomenclature to bring about with the minimum of delay some final decision as to the names of the principal animals and plants of economic importance.

Somewhat similar objections may also be raised to popular names. These are frequently of very local application and may vary considerably within the same country, or the same name may be used in widely separated parts of the English-speaking world for entirely distinct animals or plants. Since it is clear that the use of popular names must be continued under present conditions, some uniformity is highly desirable. This can only be obtained by the formation of a central body to which lists of local names both of plants and animals in use throughout the English-speaking world could be sent. It would be the duty of such a body to collect data as to all the recognised names, to reduce their number to a minimum and to compile a list that authors should agree to use as far as possible. The names selected should, where practicable, be informative and have some educational value for the layman.

In this respect much advantage might be gained in the entomological field if some agreement could be come to as to the popular names to be applied to the larval stages of different orders of insects: *e.g.* the restriction of "caterpillar" to the Lepidopterous larva, of "maggot" to the Dipterous and of "grub" to the Coleopterous. The term "worm," though objectionable as having a precise zoological significance, is in very general use especially in connection with Lepidopterous larvae infesting cotton-bolls and might be retained in this restricted sense, but limited to it. The use of misleading names such as "white ants" for "termites" should be avoided altogether. Names such as "Imported Cabbage Worm" used in North America for *Pieris rapae* are unsatisfactory as being only applicable to one part of the English-speaking world, and "European Cabbage Caterpillar" would be better. Similar adjustments of popular names among plants are advisable in the botanical field, and many cases will at once occur to the economic botanist.

To recapitulate, the weight of evidence goes to show that the use of *both* scientific and popular names is necessary under present conditions; there are difficulties inherent in the use of either, but these arise from the same cause, *i.e.* lack of uniformity and agreement on the subject among workers throughout the world; these difficulties can and should be remedied to a considerable extent.

LAWS OF THE ASSOCIATION OF ECONOMIC BIOLOGISTS

1. The Association shall be named "The Association of Economic Biologists."

2. The objects of the Association shall be to promote the study of Economic Biology.

3. The Association shall consist of Honorary and Ordinary Members.

4. Each candidate for ordinary membership shall be nominated by two members. Such nomination shall be approved by the Council and confirmed by a vote of two-thirds of the members present and voting at the next General Meeting.

Every member elected shall receive notice from the Secretary and shall continue a member until his written resignation shall be received by the Secretary, or until membership be forfeited under the Laws.

Ordinary Members shall pay an annual subscription of One Guinea, due on January 1st of each year, or may compound for their subscription with a sum of fifteen guineas.

All Ordinary Members on first election shall pay an entrance fee of half-a-guinea.

5. Ordinary Members shall be entitled to admission to all the meetings of the Association, to vote thereat, to present papers, to take part in discussions and to receive a copy of the Association's publications.

Each member shall be entitled to introduce personally non-members to the Association's meetings.

6. Honorary Members shall be persons, *not subjects of the British Crown*, who have contributed in an eminent degree to the advancement of the science of Economic Biology. They shall be recommended by a majority of the whole Council and elected in the same manner as Ordinary Members.

The number of Honorary Members shall not at any time exceed *twelve* and not more than *two* shall be elected in any one year.

Honorary Members shall not be liable to any payments and shall each receive a copy of the Association's publications.

Their privileges shall be the same as those of Ordinary Members, but they shall not be entitled to vote at the meetings.

7. The Council shall have power, at any of their meetings, by two-thirds of the votes of those present and voting, to terminate the membership of any member whose subscription shall be one year or more in arrears, or whose membership shall, from any other cause, be undesirable. No member whose subscription is in arrears shall be entitled to vote at a General Meeting or to receive the Association's publications, nor shall any publication be sent to a new member until his entrance fee and subscription shall have been received.

8. All meetings shall be announced by circular addressed to all Members resident in the United Kingdom. The place and time of the meetings shall be decided by the Council; ten shall be a quorum at such a meeting.

9. An Annual General Meeting shall be held and shall ordinarily be the General Meeting falling nearest to the end of the year or as the Council shall decide.

At this meeting the order of business shall be:

1. The reading of the minutes of the previous meeting.
2. The [illegible]ng of a report of the Council on the work of the past year.
3. The statement of the Treasurer.
4. The election of members.
5. The election of Officers and other members of the Council.
6. Other business.

10. The business of the Association shall be conducted by a Council consisting of a President, not more than five Honorary Vice-Presidents, a Treasurer, one or more Secretaries, and twelve other members.

11. The Council shall nominate the Officers and other Members of the Council for the ensuing year. A list of such nominations shall be sent to all members resident in the United Kingdom at least three weeks before the Annual General Meeting. The President shall designate two Members of Council to act as Vice-Presidents.

Any Member proposing an addition to, or an alteration in the list must inform the Honorary Secretary by letter at least ten days before the Annual General Meeting.

The nominations shall be confirmed by the members present at the Annual General Meeting and a ballot shall be taken in the event of any additions or alterations being proposed.

12. The Council may fill up any vacancy that may occur in the list of Officers and Council.

13. The Council shall meet at such times as they may determine; six members shall form a quorum.

The Council shall purchase such books, instruments, specimens, furniture and other necessaries as may be required, pass the accounts and authorise their payment, and generally manage the affairs and administer the funds of the Association.

14. The Council shall appoint from the Members of the Association an Editorial Committee who shall be responsible for the publications.

15. At a Council Meeting, prior to the Annual General Meeting, the Council shall appoint one or more Auditors to audit the Treasurer's Accounts.

16. All properties of the Association, both present and future, shall be deemed to be vested in the Council of the Association for the time being, in conformity with the provisions of the Literary and Scientific Institutions Act, 1854.

17. No new Law shall be made nor any Law altered except on the proposition of the Council or the requisition of at least ten members addressed to the Honorary Secretary. The new Laws or alterations of Laws shall be proposed in writing, signed by the requisitionists and delivered to the Honorary Secretary a month before an Extraordinary General Meeting, which shall be called for the purpose.

Such proposed new Laws or alterations in the Laws shall be printed in the circular convening the Meeting, and sent to all members resident in the United Kingdom at least two weeks before the date of such Meeting.

No new laws, alterations or amendments shall be passed except by a two-thirds majority, when not less than fifteen members are present and voting.

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